THE UNIVERSITY OF ALBERTA

CLASSIFICATION, PHYLOGENY, AND BIOGEOGRAPHY
OF THE EUXOA DETERSA GROUP
(LEPIDOPTERA: NOCTUIDAE)

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Classification, Phylogeny, and Biogeography of the *Euxoa detersa* group (Lepidoptera: Noctuidae)" submitted by J. Donald Lafontaine in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Abstract

Thirty-one species and two subspecies are included in the detersa group of the genus Euxoa (Lepidoptera: Noctuidae). Two species are described as new: Euxoa castanea Lafontaine, new species, type locality - Golden, British Columbia; Euxoa inscripta Lafontaine, new species, type locality - Craig, Colorado. All 31 species in the E. detersa group are distributed in western North America; the ranges of four of these extend into eastern North America.

In North America, Euxoa includes about 180 species in 65 species groups and 7 subgenera (two unnamed). In the Palearctic region, the genus includes about 100 species in 4 subgenera and about 20 species groups. Few species are distributed south of northern Mexico, northern Africa and northern India. A North American origin for the genus in mid-Tertiary time is most probable, based on specializations of the genus for aridland living.

A phylogeny of the E. detersa group is preceded by a reconstructed phylogeny of species groups and subgenera of Euxoa and an evaluation of structural characters.

For biogeographical analysis, species are arranged in groups according to habitat; these are 17 aridland species and 13 forest species. Aridland species are distributed primarily in grassland areas in the Great Plains and in sagebrush areas or piñon-juniper woodland in the intermontane region. Ranges in these two regions are connected in arid corridors through the Rocky Mountain region from southwestern Montana to northeastern Idaho, southwestern Wyoming to

northeastern Utah, and in New Mexico south of the Sangre de Cristo Mountains. Forest species are arranged in two groups: those that occur in both conifer forests and piñon-juniper woodland (5 species), and those that occur only in conifer forests (8 species). Species in the former category occur throughout the mountain ranges of the west including those of the Great Basin wherever suitable habitat occurs. Those of the latter category occur in conifer forests on mountain ranges around the Great Basin but do not occur in the Great Basin, even in mountain ranges that support suitable habitat. Most forest species that are distributed in the Rocky Mountain region occur in disjunct woodland areas in the Great Plains.

The effect of Wisconsinan glaciation on the biogeographic regions of western North America is reconstructed from a review of fossil pollen and plant macrofossil studies. From this synthesis, it is suggested that during the Wisconsinan glacial maximum, conifer forests and conifer forest species were widely distributed in the Great Plains south of the Laurentian ice sheet, and at low elevations in the Sierra Nevada and Rocky Mountain regions. Although piñon-juniper woodland, and species associated with this habitat, were widespread in the Great Basin during the last glacial maximum, conifer forests of pine and fir on mountain ranges of the Great Basin remained disjunct. Forest species that do not occur in piñon-juniper woodland were distributed around the Great Basin but were prevented from reaching suitable habitat in mountain ranges within the Basin by unsuitable habitat in the intervening lowlands. The ranges of aridland species were greatly reduced during Wisconsinan time. In the Great Plains, aridland

species probably occurred in piñon-juniper woodland in the Wyoming Basin, in the southwestern Great Plains and in the Chihuahuan desert. Some species occurred in the Nebraska Sandhills and in eastern Texas. In the intermontane region aridland species occurred in piñon-juniper woodland in the Great Basin and the Mojave Desert. Aridland corridors through the Rocky Mountains were eliminated during the Wisconsinan glacial maximum.

The possibility of speciation during Wisconsinan time is reviewed. Although the distribution of many sister species are what would be expected from speciation during the Wisconsinan, the distributions may reflect allopatric distributions during Wisconsinan time and not speciation.

Future research on the _E. detersa_ group should concentrate on several aspects of the way of life of the larvae. Information about soil and hostplant specificity of the larvae would contribute much to our understanding of distribution patterns, resource partitioning, and interspecific competition.

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1. Introduction

The genus Euxoa has a notorious reputation for the difficulty encountered in identifying constituent species. This notoriety stems from three factors: the large number of species, structural uniformity among species, and high degree of intraspecific variability.

In this paper, a revision of the Euxoa detersa group, the largest species group in the genus, is presented. Thirty-one species and two subspecies are included in the group. Classification, phylogeny and biogeography of the E. detersa group are treated in detail. More generalized discussions on phylogeny, distribution, origin, and bionomics of the genus are included.

1.1. Historical review

A review of taxonomic work on Euxoa in North America was given by Hardwick (1970a). In the latter half of the nineteenth century, workers in both Europe and North America described many new species of noctuids. Many new species were named on the basis of peculiarities in color or maculation. The genus Euxoa was particularly susceptible to a proliferation of names because of polymorphism and geographical variation in wing color in many species.

In the twentieth century, the use of male genitalia as a taxonomic tool was an important advancement that allowed many taxonomic problems to be resolved and correct synonymies to be established in many genera. In Euxoa, however, structural uniformity, coupled with the large number of species and available names kept the genus in a state of confusion. The fact that Euxoa could not be subdivided in smaller, more manageable monophyletic units seriously hampered revisionary work on the genus.

Revision of Euxoa of the Soviet Union by Kozhanshikov (1929, 1937) was a significant step forward in that both male and female genitalia were used. In North America it was not until 1950 that female genitalia were used in revisionary work on Euxoa. At that time McDunnough (1950) emphasized characters of the female genitalia in a revision of eastern North American species.

A breakthrough in Euxoa systematics came when Hardwick (1970a) demonstrated the taxonomic value of the male vesica.

Hardwick was able to show that characters of the male vesica could be used to arrange species of Euxoa into subgenera and species groups as well as to resolve taxonomic problems among closely related species. Subdivision of Euxoa into subgenera and species groups initiated a series of studies on individual species groups (see papers by Hardwick and Lafontaine).

1.2. Distribution of the genus

In general, Euxoa is distributed in dry regions of the northern hemisphere. The genus is most diverse in North America, particularly in the west; it consists of about 180 species in 65 species groups and 7 subgenera (see Lafontaine, 1980 and chapter 4).

In the Old World, about 70 species occur in the Soviet Union, Mongolia and China. To this total additional species can be added from Kashmir, India, and Nepal (8 species), the Middle East (4 species), Europe (10 species) and northern Africa (10 species) (Boursin, 1940a, 1940b, 1944, 1952, 1964; Hartig and Heinicke, 1973; Kovaks and Varga, 1973; Kozhantschikov, 1929, 1937).

The Palearctic fauna, consisting of approximately 100 species, can be arranged into about 20 species groups (most of which also occur in North America) and 3 subgenera (all of which also occur in North America). Few species of Euxoa occur south of northern Africa, northern India and northern Mexico.

Although about 24 species of Euxoa were formerly thought to occur in South America (e.g. Köhler, 1945; Kozhantshikov, 1937), all but two of these have now been transferred to other genera (see Köhler, 1955, 1967). The status of the two South American Euxoa species remains unclear.

1.3. Origin of the genus *Euxoa*

In the absence of a fossil record for Noctuidae (see Wilson, 1978a; Skalski, 1976) other evidence must be considered to establish a possible time of origin of *Euxoa*.

The Lepidoptera are generally believed to have arisen some time between the Triassic and the Early Cretaceous (Shields, 1976; Whalley, 1978). The oldest known Lepidoptera fossils are Lower Cretaceous and consist of a species of Micropterygidae and a probable species of Incurvariidae (Whalley, 1978). Since most families of Lepidoptera were probably present by the Oligocene (Shields, 1976; Common, 1975; Wilson, 1978a, 1978b), radiation of the order must have occurred during Late Mesozoic or Early Tertiary times, even though most known Late Cretaceous fossil Lepidoptera specimens belong to primitive groups (Wilson, 1978b; Whalley, 1978). Speculation, based on distribution patterns, indicate an earlier radiation of families (see Shields, 1976). Later arguments by Shields and Dvorak (1979), which expanded on this theme, are weak because of a lack of a substantiating phylogenetic analysis.

The "higher noctuids", particularly cutworm genera adapted to desert and grassland conditions, probably originated, or at least radiated, during the period when such habitats were developing in the world. Desert and grassland habitats began to develop in late Oligocene and Miocene times (Cracraft, 1973; Axelrod, 1976). Desert flora and aridland avifauna are believed to have evolved during the Miocene (Hubbard, 1973) as did such grassland mammalian families as Bovidae (cattle, antelope, goats) and Antilocapridae (pronghorn) (Romer, 1966). The Miocene is also the period of origin of grazing horses (Simpson, 1951) and aridland katydids (Cohn, 1965). Although grass pollen is first recorded from Upper Cretaceous (Maastrichtian) deposits in West Africa "grasses do not become frequent in the fossil record until the Lower Eocene, probably correlated with the rise of grazing mammals and the origin of non-bambusoid tribes of grasses" (Raven and Axelrod, 1974, p. 395).

Based on this information, aridland cutworm genera, including Euxoa, are assumed to have arisen during the middle Tertiary.

Any statement on the place of origin of Euxoa must be considered tentative until a thorough phylogenetic analysis of Palearctic species has been done. A preliminary analysis of the phylogenetic relationships of the Nearctic and Palearctic species leads me to suggest that the genus originated in North America. Most species groups that occur in the Old World belong to the highly derived lineages of the subgenus Euxoa (i.e. lineages 11 and 13, Fig. 199) and to the subgenus Orosagrotis. The subgenus Chorizagrotis also occurs in the Palearctic region. This, however, is not surprising since the subgenus contains migratory species. One species of the subgenus in North America occurs as far north as Greenland and Alaska (Hardwick, 1970a). Phylogeny of Euxoa in North America is discussed in chapter 4.

1.3.1. Origin of the *Euxoa detersa* group

Other than the general argumentation outlined above for a mid-Tertiary time of origin for *Euxoa*, little can be said regarding time of origin of the *Euxoa detersa* group, other than that it was probably in Neogene time.

The sister group of the *E. detersa* group (see figure 199) is not helpful for determining a place of origin of the *E. detersa* group (other than that it was somewhere in the Holarctic region), since it consists of species groups that occur in both the Nearctic and the Palearctic regions.

The *E. detersa* group, as well as about 50 species groups and 3 subgenera of *Euxoa* are apparently restricted to the Nearctic region. The diversity of the Palearctic *Euxoa* fauna, as compared to that of the Nearctic region, suggests that either relatively few New World species groups reached the Old World, or many species groups have gone extinct there. The former hypothesis is considered more likely because the Palearctic *Euxoa* fauna is primarily a subtraction fauna of Nearctic groups consisting mainly of more northerly Holarctic species groups.

Based on these data, a North American origin of the *E. detersa* group is considered to be the most probable hypothesis.

1.4. *Euxoa* survey

Long series of specimens from a large number of localities are required for revisionary work on a taxonomically difficult genus. Such material is also invaluable for clarifying distribution patterns and in determining habitat preferences for species. To these ends, a survey of *Euxoa* species in western North America was initiated in 1960 by D.F. Hardwick of the Biosystematics Research Institute, Ottawa. Approximately 50,000 specimens have been collected to date; collecting localities are shown in figure 186. At each collecting site, detailed habitat notes and photographs were taken; these were used to establish habitat preferences and tolerances of *Euxoa* species. These specimens when added to the holdings of the Canadian National Collection (CNC) form a sample of approximately 80,000 specimens of *Euxoa*. About 12,000 of these specimens are species in the *Euxoa detersa* group. Most collections were made during August and September, the period in which the majority of *Euxoa* species are flying. Distribution of spring flying species remain poorly known.

1.5. Cutworm bionomics

Larvae of *Euxoa* species, as well as those of many other noctuid genera, are commonly called cutworms. Cutworm ecology is a field of study that has received little attention. This is surprising considering both the total number of species involved and the economic importance of many species. Problems in identification is probably the main factor that has hampered ecological work on cutworms. Only one book (i.e. Crumb, 1956) attempts to treat all North American noctuid larvae; this work includes about 700 species, approximately one-fifth of the North American fauna. Unfortunately, Crumb could find no characters that could be used in identification of larvae of *Euxoa* species.

Most papers on cutworm bionomics treat only a single species, usually an economically important one, and contain only larval descriptions and life history information. A notable exception to this is a series of papers on bionomics of the pale western cutworm (*Agrotis orthogonia* Morr.) by H.L. Seamans, W.C. Cook, and L.A. Jacobson (see Jacobson, 1971, for review). Unfortunately, comparable information on other cutworm species is lacking, although there is a fair amount of piecemeal ecological information on some pest species.

Cutworms are usually categorized as being subterranean, surface-feeding, or climbing cutworms. The larvae of most species of *Euxoa* are surface-feeding cutworms, although those of a number of species readily adopt a climbing habit (Hardwick, 1970a).

Many factors of the physical environment are important to cutworm bionomics. Probably the three most important factors are temperature, soil moisture, and soil texture. Temperature is important in controlling rates of metabolism and development, limits of distribution both northward and southward, and number of generations per year. Many cutworms, including species of *Euxoa*, aestivate through summer heat in an earthen cells in the soil. Since there is a limit to the amount of heat that they can tolerate, their southern limit is probably controlled by summer temperature (Hardwick and Lefkovitch, 1971). In general, larvae of species that occur in open aridlands have a longer prepupal aestivation than do those of species that occur in forested areas (J.R. Byers, *Pers. com.*). Soil moisture and soil texture tolerances and preferences of cutworm larvae are known for few species but these factors are undoubtedly important in determining distribution patterns and in resource partitioning. The importance of soil conditions to plant distributions has recently been recognized (e.g. see Kruckeberg, 1969; Zamora and Tueller, 1973).

In chapter 5, ranges of many *Euxoa* species are compared with those of plant species and communities (e.g. species associated with sagebrush areas or conifer forests). Since larvae do not utilize these plants as food, it is assumed that the association is due to similarities in habitat requirements rather than to a direct dependence of the noctuid on the plant. A possible exception to this is that many aridland *Euxoa* species occur in areas where rabbitbrush (*Chrysothamnus* spp.) is abundant. Although this association could be attributed to a preference for arid habitats in both cutworms and rabbitbrush, it is probably also related to adult feeding requirements. In many arid regions, rabbitbrush is one of few plants in bloom in the fall when adults of Euxoa species are flying; its flowers are an essential food source for the moths. The flight of fall noctuids in many arid regions is strongly correlated with flowering time of rabbitbrush (Cook, 1930b).

The most interesting aspect of cutworm bionomics, and the one that has recieved the least attention, is resource partitioning by larvae. Although larvae of most species are general feeders, they usually show a preference for either broad-leaved herbs or grasses (e.g. see Strickland, 1948). Except for a knowledge of a few basic factors in niche segregation (e.g. subterranean vs. surface-feeding; broad-leaf eating vs. grass-eating; and moisture loving vs. dry soil species) knowledge of cutworm bionomics is in a very crude state. Walkden (1943) found that fields that differ in plant composition also differ in cutworm composition. Unfortunately, soil conditions were not considered as a possible factor affecting species composition.

Experiments on the effects of such factors as temperature, moisture and soil conditions on cutworm bionomics are badly needed. An understanding of the effects of these variables will greatly enhance our knowledge of resource partitioning and geographical distribution of cutworm species.

2. Materials and methods

2.1. Materials

During this study, approximately 16,000 specimens were examined. Most specimens (about 12,000) are in the Canadian National Collection (CNC), Ottawa. This material was supplemented by specimens from the private collections of Mr. A. Blanchard, Houston, Texas, Dr. J.G. Franclemont, Ithaca, New York, Mr. J.R. Heitzman, Independence, Missouri, Mr. M.C. Nielsen, Lansing, Michigan, Dr. R.W. Poole, Providence, Rhode Island and from collections in the following institutions:

The American Museum of Natural History (AMNH), New York, New York (Dr. F.H. Rindge).

The California Academy of Sciences (CASC), San Francisco (Dr. D.H. Kavanaugh).

California Department of Agriculture (CDAE), Sacramento (Dr. T.N. Seeno).

Cornell University (CU), Ithaca, New York (Dr. J.G. Franclemont).

North Dakota State University (NDSU), Fargo (Dr. E.U. Balsbaugh Jr.).

Los Angeles County Museum of Natural History (LACM), Los Angeles, California (Dr. C.L. Hogue).

San Diego Natural History Museum (SDMC), San Diego, California.

The United States National Museum of Natural History (USNM), Washington, District of Columbia (Dr. E.L. Todd).

Peabody Museum of Natural History (PMNH), Yale University, New Haven, Connecticut (Dr. C.L. Remington).

2.2. Methods

2.2.1. Collecting and preparation of material

Collecting. Adult moths were collected by using a light trap with a 125-watt, Osram, mercury vapor bulb as light source. The design of the light trap used was described by Hardwick (1968).

Preparation of material. Specimens were pinned in the field and later spread following the technique described by Martin (1977).

Genitalia preparations were made following the technique described by Hardwick (1950) with one modification. The male vesica was everted by squirting isopropyl alcohol through it while immersed in a dish of isopropyl alcohol rather than while immersed in a 10 per cent alcohol solution.

Ovipositor valves of some females were separated from the remainder of the genitalia and mounted flat. This was done by cutting the membrane anterior to the valves and between the valves ventrally. The valves were then mounted in an outspread condition. This allowed valve shape and setae to be studied more readily.

2.2.2. Structural characters

There is a frustrating paucity of structural characters that can be used to characterize adults of species of Euxoa other than those of the genitalia.

Males of most species have biserrate antennae, although those of a few species groups can be characterized by antenna structure. Males of three species groups have plumose antennae; those of two species groups have filiform antennae.

A frontal tubercle is present in adults of all species of Euxoa except for five. Species that are without a frontal tubercle live in sandy areas; adults of these species presumably do not have difficulty in escaping from the subterranean pupal cell after eclosion.

Adults of most species have rounded, globular eyes. Those of some species that live in arctic or alpine areas have reduced, elliptoid eyes.

Of the above three external structural characters, only one is of use in distinguishing species in the Euxoa detersa group; a frontal tubercle is absent from most specimens of Euxoa detersa (Walker).

Male genitalia possess many structural characters that are of taxonomic and phylogenetic importance. Within Euxoa, size and shape of sacculus, sacculus extensions, cucullus, harpe, juxta and uncus are all important characters. Of these structures, sacculus extensions and harpes are most useful for distinguishing species of the E. detersa group, although other structures may be important in specific instances. The most useful structure of the male genitalia, both within the *E. detersa* group and *Euxoa* in general, is the vesica. Overall vesica shape, as well as shape and position of accessory pouches, provide excellent characters for taxonomic and phylogenetic studies.

Female genitalia have several structural characters that have proven to be very useful. Many closely related species that are indistinguishable by structures of male genitalia can be distinguished by those of female genitalia and vice versa. The most useful character for phylogenetic studies and for distinguishing species groups is shape of bursa copulatrix. Shape of ovipositor valves, their vestiture, and presence or absence of sclerotized projections, are useful characters for distinguishing species. In females of some species groups sclerotized plates in the dorsal and ventral wall of ductus bursae, and anterior apophyses, may be used to distinguish species.

Taxonomic value of structural characters of *Euxoa* were reviewed by McDunnough (1950) and Hardwick (1970a).

2.2.2.1. Measurements

Genitalia measurements were made with a Leitz stereoscopic microscope at 12.5X magnification using a micrometer eyepiece with a scale interval of 0.025 mm.

Length of four structures of male genitalia were mearured: right sacculus extension, left sacculus extension, right harpe, and right sacculus. From these data, mean and standard deviation were calculated. A diagrammatic presentation of how these measurements are taken was given by Hardwick and Lefkovitch (1973).

In addition to genitalia measurements, two wing measurements were taken. "Expanse" is the distance between apices of the forewings of spread specimens. This distance varies slightly, depending on how a specimen is spread so not all specimens were included. "Length of forewing" is length of right forewing from base to apex.

2.2.3. Maculation

Maculation of Noctuidae was described in detail by Forbes (1954); only a brief review is included here.

Specimens with maculation complete (e.g. see fig. 47) have six transverse lines crossing the forewing; basal line, transverse anterior line, median line, transverse posterior line, subterminal line, and terminal line. The basal line, near wing base, is extended only half way across the wing in most species. Transverse anterior and transverse posterior lines are double lines; they are present and conspicuous in most species. The median line consists of a dark shade that crosses the forewing between reniform spot and orbicular spot close to the transverse posterior line. In most species, the subterminal line is a pale line made evident by dark shading in the terminal area and by dark sagittate spots proximal to it in the subterminal area. The terminal line is along the outer edge of the forewing.

The area of the forewing is divided into four smaller areas. The basal area is between wing base and transverse anterior line; the median area is between transverse anterior and transverse posterior lines; the subterminal area is between transverse posterior line and subterminal line; and the terminal area is between subterminal and terminal lines. The basal area has a black, basal dash in many species (e.g. see fig. 9). The median area has three spots in most specimens (e.g. see fig. 47), a rounded "orbicular spot", a kidney-shaped "reniform spot", and an elongate "claviform spot" distal to the transverse anterior line. The terminal area is dark in most species.

The cubital vein (Cu) of the forewing is just below the orbicular and reniform spots; it branches into four veins, M_2, M_3, Cu_1, and Cu_2. In many species, veins Cu, Cu_1 and M_3 are pale-lined and contrast with the ground color of the forewing (e.g. see fig. 51).

The hind wing has a dark, crescentic, discal spot in many species. In some species, a trace of a median line is present on the dorsal surface; this line is parallel to the outer edge of the wing about 2/3 from wing base (e.g. see fig. 13). A median line on the ventral surface of the hind wing is present in most species.

2.2.4. Description format

The description format used follows that of Hardwick (1970a), and includes: synonymy and selected bibliography; description of adult; type material; distribution and period of flight; habitat; and remarks. A list of material examined is not included but collection data is summarized in the discussion on distribution and period of flight.

Descriptions of adults are presented in the following sequence: vestiture of head and thorax; ground color of forewing; transverse lines; areas of forewing; spots, dashes and streaks on forewing; expanse; male genitalia; female genitalia.

Structures of male genitalia referred to most frequently in descriptions are shown in figure 65.

2.2.5. Habitat descriptions

Habitat descriptions were prepared by using both field notes and photographs from each collecting site shown in figure 186. At any one locality, such material is of little use since it can not be determined which portion of the collecting area a given specimen came from. Over a large number of localities, however, a picture begins to emerge as to what conditions must be present for each species to occur in an area. Some species, for example, which were frequently collected in pine forests in montane areas were collected in the Great Plains only at localities where a pine forest was nearby. These species are assumed to occur only in pine forests and not in treeless plains. Other species occur only where coarse, loose, soil is present and are found in the Great Plains only in areas of heavy erosion such as badlands and river terraces.

Although habitat diagnoses obtained in this way are crude, they have proven to be useful in interpreting distribution patterns.

A more refined knowledge of habitat preferences for each species must await field studies of larval habits (see chapter 1.5).

2.2.6. Sorting of specimens

Specimens were initially sorted into more or less homogeneous populations by using wing color and maculation, geographical distribution, and period of flight. These population samples were then studied more critically by using structural characters and were arranged into more inclusive units. It was then determined whether these groupings represented species, subspecies, or geographical populations.

Male and female specimens of each species are similar in wing pattern so no difficulty was encountered in associating both sexes of each taxon.

After limits of variation of each species had been established, specimens of each were arranged geographically to study geographical variation.

To facilitate taxonomic treatment and discussion, species were arranged into species groups. Species groups are monophyletic groups of structurally similar species that share a derived character state that distinguishes its members from those of other species groups. The rank of species group is informal. Taxa belonging to the *Euxoa detersa* group are revised in this paper; other species groups are discussed in chapter 4.3, phylogeny of species groups of *Euxoa*.

2.2.7. Criteria for species and subspecies

"Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Simpson, 1961, p. 150).

In practice, presence or absence of reproductive isolation can rarely be demonstrated, especially when preserved material is all that is available. Also, such a rigid definition is frequently inadequate for species in which reproductive isolation occasionally breaks down (e.g. see Byers and Hinks, 1978; Teal et al., 1978). In these instances, Simpson's evolutionary definition of a species is more appropriate. "An evolutionary species is a lineage ... evolving separately from others and with its unitary evolutionary role and tendencies" (Simpson, 1961, p. 153).

"A subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species and differing taxonomically from other populations of the species" (Mayr, 1969, p. 41). There has been much discussion among taxonomists as to what constitutes a subspecies (see discussion by Mayr, 1969). Some taxonomists recognise subspecies only for allopatric populations of uncertain status (e.g. Whitehead, 1972); others, at the opposite end of the spectrum, consider every population that differs in any way from neighboring populations to be a subspecies. While a proliferation of names for local populations is undesirable for many reasons, the subspecies taxon is useful if applied judiciously.

I use two criteria for deciding whether or not a subspecific name is warranted. The degree of phenotypic difference between subspecies should approach that found between species of the same or related groups; the phenotypic differences are the result of isolation and differentiation, not simply the effect of local conditions on phenotypic expression of the gene pool. In addition, I use subspecific names only if they facilitate discussions on biogeography.

For example, specimens of *Euxoa detersa detersa* and *Euxoa detersa personata* appear to be as different from each other as are those of *Euxoa detersa* from those of *Euxoa cicatricosa*. The differences between these two aggregates of populations are found over a variety of comparable habitats. The two subspecies were probably isolated in different geographical regions during the last glacial maximum. Since *Euxoa detersa personata* occurs in the Great Lakes region, the Great Plains, and the boreal forest, a vernacular name such as the "Great Plains" populations is not convenient, further, the subspecific name draws attention to the distinctness of the two aggregates of populations.

On the other hand, specimens of *Euxoa cicatricosa* look different in various parts of the range of the species. The differences, however, are in wing color which matches the color of the substrate where the moths occur. Subspecific names for such populations cannot be justified. Inbreeding of some color forms of *Euxoa* species has produced forms typical of specimens from other regions (J.R. Byers, *pers. com.*). These experiments indicate that habitat associated color forms are the effect of local conditions on phenotypic expression of the gene pool; such ecotypic forms could change rapidly in different habitats.

2.2.8. Geographical variation

An excellent review of this topic was given by Hubbell (1956). In adults of *Euxoa*, geographical variation in wing color is a common phenomenon in many species. This has two components in most species: color or hue and shade or degree of darkness. Wing color varies with substrate color in many species: brown forms occur in the east and north; buff, or pale gray forms occur in the Great Plains and northern Great Basin; and reddish orange forms occur in red sandstone areas of the southwest. In shade, specimens tend to be pale in hot, arid regions and dark in cool, mesic regions.

Some geographical variation cannot be explained in terms of local conditions but is the result of isolation and differentiation of populations (see section 2.2.7.). In many species geographical variation of this type consists of differences in wing pattern rather than color.

Geographical variation in structural characters is rare in *Euxoa* species. In some species length of sacculus extension in male genitalia varies in different parts of the species range (e.g. *Euxoa punctigera* (Wlk.), see Lafontaine, 1974c). Within the *Euxoa detersa* group, geographical variation in structural characters has only been found in shape of female ovipositor valves of three species (*E. castanea* Laf., n. sp., *E. idahoensis* (Grt.), *E. quadridentata* (Grt. & Rob.); it is discussed under those species.

2.2.9. Immature stages

Immature stages were not used in taxonomic or phylogenetic analyses. The reason for this is that immature stages are known for too few species, and those that are known lack characters suitable for such analyses.

Eggs of two species in the *Euxoa detersa* group (*E. servita* (Sm.), *E. detersa* (Wlk.)) have been described (Salkeld, 1975).

Larvae of only one species in the *Euxoa detersa* group (*E. detersa* (Wlk.)) have been described, although those of four other species (*E. castanea* Laf., n. sp., *E. auripennis* Laf., *E. niveilinea* (Grt.), *E. cicatricosa* (Grt. & Rob.)) have been reared (Hinks and Byers, 1976).

At present, no characters have been found with which larvae of *Euxoa* species can be differentiated (Crumb, 1956).

3. Classification

3.1. The Euxoa detersa group

Description. Antenna of male varied from slightly to moderately biserrate and bifasciculate. Frontal tubercle present except in most specimens of *E. detersa*.

Maculation of forewing complete in species that lack longitudinal streaking; transverse lines obscure or absent in species with longitudinal streaks on forewing.

Male genitalia. Valves bilaterally symmetrical or slightly asymmetrical with respect to lengths of sacculus extensions; left sacculus extension slightly shorter than right in many specimens. Right sacculus extension slightly to markedly longer than right harpe in most species; markedly shorter in one species (*E. melura*). Sacculus extensions about as stout as harpes to slightly stouter. Vesica bent to right or dorsally above apex of aedeagus. Sub-basal diverticulum foot-shaped in most species; somewhat triangular in some species (e.g. *E. costata*), small and horn-like in males of *E. citricolor*. An additional nipple-like diverticulum on vesica sub-basally in some species. Median diverticulum horn-shaped, basal bulge directed toward sub-basal bend present in some species; median diverticulum near sub-basal bend in most species but positioned about half way to apex in some species. Apical diverticulum in most species. Angle formed by apical half of aedeagus with respect to apical half of vesica 20-85°; 40-50° in most species.

Female genitalia. Bursa copulatrix unisaccate; corpus bursae oval or somewhat rectangular, slightly invaginated on left side in females of some species; ductus bursae entering corpus bursae 1/4 to 1/2 way along right side. Sclerotized plates in dorsal and ventral walls of ductus bursae extended anteriorly slightly farther than anterior apophyses, except in females of *E. quadridentata*. Ovipositor valve clothed with fine setae; long stout setae, sclerotized apical projections, or short conical setae in some species. Subbasal row of long, thin setae in most species. Ovipositor valves rounded or triangular in shape; dorsal margins not fused.

Remarks. The *E. detersa* group consists of 31 species, all confined to North America: *E. costata* (Grote), *E. castanea* Lafontaine, new species, *E. foeminalis* (Smith), *E. idahoensis* (Grote), *E. clausa* McDunnough, *E. brevipennis* (Smith), *E. servita* (Smith), *E. redimicula* (Morrison), *E. auripennis* Lafontaine, *E. arizonensis* Lafontaine, *E. olivalis* (Grote), *E. agema* (Strecker), *E. oblongistigma* (Smith), *E. citricolor* (Grote), *E. tronella* (Smith), *E. teleboa* (Smith), *E. moerens* (Grote), *E. latro* (Barnes and Benjamin), *E. murdocki* (Smith), *E. dodi* McDunnough, *E. infracta* (Morrison), *E. laetificans* (Smith), *E. quadridentata* (Grote and Robinson), *E. inscripta* Lafontaine, new species, *E. unica* McDunnough, *E. niveilinea* (Grote), *E. dargo* (Strecker), *E. melura* McDunnough, *E. detersa* (Walker), *E. cicatricosa* (Grote and Robinson), *E. recula* (Harvey). Two species, *E. detersa* and *E. quadridentata* consist of two subspecies: *E. d. detersa* (Walker), *E. d. personata* (Morrison); *E. q. quadridentata* (Grote and Robinson), *E. q. flutea* Smith.

Members of the E. detersa group may be distinguished from those of other species groups by a combination of male and female genitalic characters. These are: elongate sacculus extensions and vesica shape in males; unisaccate, oval corpus bursae with ductus bursae on right side, and ovipositor valves not fused together in females.

All members of the E. detersa group are found in western North America; ranges of four species extend into eastern North America as well.

3.2. Key to males of *Euxoa detersa* group

1 Right harpe at least 1 1/4 times length of right sacculus extension (Fig. 92) .... *E. melura* McD. (p. 121).

1' Right harpe less than 1 1/4 times length of right sacculus extension 2

2 (1') Apical half of harpe microscopically pubescent, in addition to much larger scattered setae 3

2' Apical half of harpe without pubescence, only larger scattered setae present, these about half as long as diameter of harpe 8

3 (2) Orbicular spot elongate, bar-like, two or three times as long as wide; right harpe less than 1.2 mm long 4

3' Orbicular spot rounded or oval; elongate in some specimens in which it is fused with pale costa, if so, then right harpe more than 1.3 mm long 6

4 (3) Right sacculus extension about 1 1/2 times length of right harpe (Fig. 75) .... *E. olivalis* (Grt.) (p. 73).

4' Right sacculus extension about 1 1/4 times length of right harpe (Fig. 76) 5

5 (4') Forewing with costa pale, evenly colored, pale shading extended uninterrupted to cubital vein on basal quarter of wing (Figs. 31. 32) .... *E. oblongistigma* (Sm.) (p. 78).

5' Forewing with costa brown like remainder of wing, not evenly colored; costal shading not extended to cubital vein near base of wing but separated from it by several light and dark lines (Figs. 28, 29) ... . *E. agema* (Stkr.) (p. 76).

6 (3') Forewing with black basal dash (Figs. 49, 50) .... *E. laetificans* (Sm.) (p. 101).

6' Forewing without black basal dash 7

7 (6') Right sacculus extension more than 1 1/2 times length of right harpe; forewing dark brown with copper colored basal and subterminal areas (Fig. 48) .... *E. infracta* (Morr.) (p. 99).

7' Right sacculus extension less than 1 1/2 times length of right harpe; forewing light brown or gray (Fig. 47) .... *E. dodi* McD. (p. 97).

8 (2') Clavus prominent, sclerotized, much longer than wide; dorsal margin of sacculus invaginated at base of clavus (Fig. 93) 9

8' Clavus inconspicuous and at most only slightly sclerotized; dorsal margin of sacculus not invaginated at base of clavus 12

9 (8) Forewing without veins Cu_1 and M_3 pale-lined and projected into terminal area (Fig. 61); distributed from Great Plains eastward to Great Lakes region .... *E. detersa personata* (Morr.) (p. 127).

9' Forewing with veins Cu_1 and M_3 pale-lined and projected into terminal area; distributed either in eastern North America, or from western Great Plains westward 10

10 (9') Distributed in eastern North America .... *E. d. detersa* (Wlk.) (p. 127).

10' Distributed from western Great Plains westward 11

11 (10') Pale areas of forewing white, cream-colored, or pale orange-brown (Figs. 62, 63); distributed throughout intermontane region and western Great Plains (Fig. 184) . ... *E. cicatricosa* (Grt. & Rob.) (p. 128).

11' Pale areas of forewing yellow (Fig. 64); distributed in southern and western portions of intermontane region (Fig. 185) .... *E. recula* (Harv.) (p. 133).

12 (8') Forewing without basal dash, not longitudinally streaked 13

12' Forewing either with black basal dash, or longitudinally streaked, particularly on veins Cu, Cu_1 and M_3, or both 18

13 (12) Right sacculus extension about as long as, or shorter than, right harpe (Fig. 80) ...... *E. teleboa* (Sm.) (p. 87).

13' Right sacculus extension longer than right harpe 14

14 (13') Basal and subterminal areas of forewing orange or yellow, median area gray (Fig. 46) .... *E. murdocki* (Sm.) (p. 95).

14' Basal, subterminal and median areas of forewing essentially same color 15

15 (14') Uncus slightly constricted at about 1/4 from apex; right harpe with 10-15 setae (Fig. 79); hind wing white in most specimens (Figs. 33-38) 16

15' Uncus dilated at middle, then tapered to apex; right harpe with 30-60 setae (Fig. 82); hind wing brown (Figs. 41-44) 17

16 (15) Forewing yellow .... *E. citricolor* (Grt.) (p. 81).

16' Forewing white or cream-colored with black dusting .... *E. tronella* (Sm.) (p. 84).

17 (15') Vesica with small nipple-like diverticulum sub-basally, in addition to normal foot-like sub-basal diverticulum; right harpe with about 30 setae; hind wing gray-brown, paler toward base in most specimens; distributed in Great Plains and Great Basin (Fig. 172) .... *E. moerens* (Grt.) (p. 90).

17' Vesica with only normal foot-like diverticulum present sub-basally; right harpe with 50-60 setae; hind wing dark brown; distributed along Cascades-Sierra Nevada axis from Washington southward to southern California, and in La Sal Mountains, Utah (Fig. 173) .... *E. latro* (B. & Benj.) (p. 93).

18 (12') Veins Cu_1 and M_3 pale-lined, contrasting, projected into terminal area 19

18' Veins Cu_1 and M_3 not pale-lined or contrasting; cubital vein pale-lined to reniform spot in some specimens but no pale-lined veins projected into terminal area 23

19 (18) Right sacculus extension at least 1 1/2 times length of right harpe (Fig. 90) .. *E. niveilinea* (Grt.) (p. 115).

19' Right sacculus extension, at most 1 1/3 times length of right harpe 20

20 (19') Vesica with **small** nipple-like sub-basal diverticulum on left side in addition to normal foot-like sub-basal diverticulum; right harpe 0.9-1.0 mm long (Fig. 91) .... *E. dargo* (Stkr.) (p. 118).

20' Vesica with only normal foot-like diverticulum sub-basally; right harpe 1.1-1.3 mm long 21

21 (20') Forewing with costal area pale, evenly colored, pale shade extended uninterrupted to cubital vein on basal quarter of wing (Fig. 51) .... *E. quadridentata* (Grt. & Rob.) (p. 104).

21' Forewing with costal area not particularly pale, or if so, then streaked and unevenly colored; costal shade interrupted from cubital vein on basal quarter of wing by a black line 22

22 (21') Ground color of forewing brown with fine black streaks on veins (Fig. 53) ... *E. inscripta* Laf. n. sp. (p. 109).

22' Ground color of forewing gray streaked with pale silver-gray (Fig. 15) .... *E. brevipennis* (Sm.) (p. 59).

23 (18') Hind wing white with **thin** black terminal line (Fig. 15) .... *E. brevipennis* (Sm.) (p. 59).

23' Hind wing shaded with brown, at least on marginal third of wing 24

24 (23') Hind wing pale with **sharply** contrasted dark marginal band on outer third 25

24' Hind wing smoky-brown, paler near base in many specimens 27

25 (24) Right sacculus extension as stout as, or thinner than, right harpe (Fig. 72) .... *E. redimicula* (Morr.) (p. 65).

25' Right sacculus extension stouter than right harpe 26

26 (25') Basal half of prothoracic collar, and costa of forewing, pale yellow-brown; forewing with transverse lines conspicuous; known only from vicinity of Saskatoon, Saskatchewan (Fig. 57) .... *E. unica* McD. (p. 112).

26' Prothoracic collar, and costa of forewing, essentially same color as remainder of forewing; forewing with transverse lines obscure, veins overlaid with black scales; distributed from southern Montana southward to Colorado and westward to Lake Tahoe, California (Fig. 53) .... *E. inscripta* Laf. n. sp. (p. 109).

27 (24') Forewing with transverse lines conspicuous; costal, subterminal and basal areas paler than median area 28

27' Forewing with transverse lines inconspicuous; subterminal and basal areas not paler than median area; costal area paler than remainder of forewing in many specimens 30

28 (27) Terminal area of forewing blurred and streaked into subterminal area; transverse posterior line not scalloped between veins (Figs. 17-19) ....

.... *E. servita* (Sm.) (p. 62).

28' Terminal area of forewing with smooth, regular inner margin; transverse posterior line scalloped between veins 29

29 (28') Distributed in northern Cordilleran region from British Columbia southward to south-central Colorado, northern Utah, central Nevada and southern California (Fig. 164) .... *E. auripennis* Laf. (p. 68).

29' Distributed in southern mountains from southwestern Colorado and southern Utah southward to central New Mexico, central Arizona and southern California (Fig. 164) .. .. *E. arizonensis* Laf. (p. 71).

30 (27') Forewing shaded with maroon or red 31

30' Forewing shaded with buff, brown or gray 32

31 (30) Forewing light red with contrasting silver-gray reniform and orbicular spots and costa (Fig. 1); distributed from British Columbia southward to southern California (Fig. 158) .... *E. costata* (Grt.) (p. 47).

31' Forewing maroon dusted with dark scales; reniform and orbicular spots either not silver-gray, or if so, then with cubital vein pale as well (Fig. 3); distributed from western Canada southward in the Rocky Mountain region to eastern Arizona and northern New Mexico (Fig. 159) .... *E. castanea* Laf. n. sp. (p. 49).

32 (30') Forewing largely black with contrasting silver-gray reniform and orbicular spots and costa (Fig. 5); distributed from northern Utah southward to Arizona and New Mexico

(Fig. 161) .... *E. foeminalis* (Sm.) (p. 52).

32' Forewing brown or with extensive brown shading, almost black in some specimens from Rocky Mountain region of British Columbia and Montana 33

33 (32') Forewing, including terminal area, yellow-buff; series of black, sagittate spots on proximal side of subterminal line; orbicular spot round; hind wing unevenly shaded with light and dark brown, dark median line in most specimens (Fig. 14); distributed in Great Plains in Alberta and Montana (Fig. 161) .... *E. clausa* McD. (p. 57).

33' Forewing dark brown in most specimens; if light buff, then terminal area dark brown with dark streaks on proximal side of subterminal line; orbicular spot oval in most specimens; hind wing evenly colored, slightly paler near base (Figs. 7-12); widespread (Fig. 160) .... *E. idahoensis* (Grt.) (p. 54).

3.3. Key to females of *E. detersa* group

1 Ovipositor valve with stout setae dorsally or apically .. 2

1' Ovipositor valve without stout setae 7

2 (1) Stout setae on dorsal margin of valve; ovipositor valve without definite row of long sub-basal setae 3

2' Stout setae primarily on apical third of valve; ovipositor valve with definite row of long sub-basal setae 5

3 (2) Stout setae scattered on dorsal margin of valve, not in single row (Fig. 155) 4

3' Stout setae in single row on dorsal margin of valve (Fig. 156); distributed from western Great Plains westward (Fig. 184) .... *E. cicatricosa* (Grt. & Rob.) (p. 128).

4 (3) Distributed east of Rocky Mountains (Fig. 183) .... *E. detersa* (Wlk.) (p. 123).

4' Distributed in western and southern intermontane region (Fig. 185) .... *E. recula* (Harv.) (p. 133).

5 (2') Long sub-basal setae on ovipositor valve stout and spike-like (Fig. 153) .... *E. dargo* (Stkr.) (p. 118).

5' Long sub-basal setae on ovipositor valve thin and hair-like 6

6 (5') Long sub-basal setae on ovipositor valve stouter on ventral portion of valve than those on dorsal portion (Fig. 154); forewing with cubital vein pale (Fig. 59) ... . *E. melura* McD. (p. 121).

6' Long sub-basal setae on ovipositor valve thin and hair-like on both ventral and dorsal portions of valve (Fig. 133); forewing with cubital vein not pale (Fig. 18) .... *E. servita* (Sm.) (p. 62).

7 (1') Sclerotized plates in wall of ductus bursae short, not extended as far anteriorly as anterior apophyses (Fig. 118) .... *E. quadridentata* (Grt. & Rob.) (p. 104).

7' Sclerotized plates in wall of ductus bursae longer, extended farther anteriorly than anterior apophyses 8

8 (7') Ovipositor valve with prominent, smooth, flange-like projection at apex 9

8' Ovipositor valve without flange, or at most, trace of flange at apex, its surface covered with minute setae 22

9 (8) Forewing either with black basal dash, or prominently streaked longitudinally, or both 10

9' Forewing without black basal dash and without longitudinal streaks 17

10 (9) Orbicular spot elongate, almost bar-like; junction of ductus bursae and corpus bursae anterior to middle of corpus bursae in most specimens 11

10' Orbicular spot round or oval; junction of ductus bursae and corpus bursae at middle, or posterior to middle ... 13

11 (10) Orbicular spot buff-filled, not outlined in white; basal dash prominent; costa evenly colored, buff or pale gray (Fig. 32) ...... *E. oblongistigma* (Sm.) (p. 78).

11' Orbicular spot with dark center in most specimens, dark center outlined in white; basal dash thin and inconspicuous; costa not evenly colored but marked with white or brown (Figs. 25-29) 12

12 (11') Forewing predominantly various shades of brown; hind wing dark brown (Fig. 29) ...... *E. agema* (Stkr.) (p. 76).

12' Forewing streaked with gray and white in most specimens; hind wing gray or brown, paler at base (Figs. 25-28) .... *E. olivalis* (Grt.) (p. 73).

13 (10') Forewing streaked longitudinally; basal dash inconspicuous if present 14

13' Forewing not streaked longitudinally; basal dash prominent 15

14 (13)[1] Cubital vein and costa pale and contrasting (Fig. 56) ... . *E. niveilinea* (Grt.) (p. 115).

14' Cubital vein and costa not particularly pale (Fig. 54) .. .. *E. inscripta* Laf. n. sp. (p. 109).

15 (13') Flange-like projection at apex of ovipositor valve rounded, about as long as wide (Fig. 135) .... *E. auripennis* Laf. (p. 68).

15' Flange-like projection at apex of ovipositor valve finger-like, longer than wide (Fig. 134) 16

16 (15') Forewing with median area heavily dusted with black (Fig.

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[1] The female of *E. unica* McD. is unknown, however, it would probably key out to this couplet.

24); distributed from Colorado and New Mexico westward 164) .... *E. arizonensis* Laf. (p. 71).

16' Forewing with median area light gray or brown (Fig. 21); distributed from Montana and Wyoming eastward (Fig. 163) .... *E. redimicula* (Morr.) (p. 65).

17 (9') Anterior end of ovipositor valve markedly produced ventrally, depth of valve greater than its length (Fig. 140) 18

17' Anterior end of ovipositor valve, at most, slightly produced ventrally, depth of valve less than its length 19

18 (17) Forewing yellow .... *E. citricolor* (Grt.) (p. 81).

18' Forewing cream-colored or pale buff, dusted with black .. .. *E. tronella* (Sm.) (p. 84).

19 (17') Ovipositor valve with raised, fin-like, sclerotized plate on posterior half of dorsal margin of valve; dorsal edge of plate straight or slightly concave, curved abruptly at anterior end to valve (Fig. 142); sclerotized plate in ventral wall of ductus bursae extended as far anteriorly as plate in dorsal wall (Fig. 111) .... *E. teleboa* (Sm.) (p. 87).

19' Ovipositor valve with rounded, or finger-like, sclerotized projection at apex, this curved around dorsal margin of valve, its dorsal edge convex and tapered anteriorly in most specimens, tapered abruptly in some specimens with sclerotized plate in dorsal wall of ductus bursae extended farther anteriorly than plate in ventral wall (e.g. 143) 20

20 (19') Forewing with median area pale gray, basal and subterminal areas orange (Fig. 46) ... *E. murdocki* (Sm.) (p. 95).

20' Forewing with basal, median and subterminal areas similar in color, if not in shade 21

21 (20') Forewing dark brown, heavily dusted with gray in most specimens; hind wing dark brown to base (Fig. 45); distributed along Cascades-Sierra Nevada axis from Washington southward to southern California; disjunct population in La Sal Mts., Utah (Fig. 173) .... *E. latro* (B. & Benj.) (p. 93).

21' Forewing light gray, light brown, or orange; hind wing gray, paler toward base in most specimens (Figs. 41-43); distributed throughout Great Plains and Great Basin (Fig. 172) .... *E. moerens* (Grt.) (p. 90).

22 (8') Forewing with prominent, black, basal dash 23

22' Forewing without basal dash 29

23 (22) Ovipositor valve with short, conical setae apically; forewing with veins Cu$_1$ and M$_3$ not pale-lined 24

23' Ovipositor valve with fine-tipped setae apically, or with veins Cu$_1$ and M$_3$ pale-lined, pale streaks projected into terminal area 28

24 (23) Forewing shaded with maroon or reddish brown 25

24' Forewing shaded with buff, brown or gray 26

25 (24) Ovipositor valve rounded or somewhat truncate apically;

forewing light reddish brown with contrasted silver-gray costa, reniform spot and orbicular spot; cubital vein not pale (Fig. 2); distributed from British Columbia southward to southern California (Fig. 158) .... *E. costata* (Grt.) (p. 47).

25' Ovipositor valve acutely angled apically; forewing maroon or chestnut-brown, dusted with black; costa, reniform spot and orbicular spot either without silver-gray shading, or with cubital vein pale as well (Fig. 3); distributed from western Canada southward in the Rocky Mountain region to eastern Arizona and northern New Mexico (Fig. 159) ... *E. castanea* Laf. n. sp. (p. 49).

26 (24') Forewing extensively black with contrasted silver-gray reniform and orbicular spots and costa (Fig. 6); distributed from northern Utah southward to New Mexico and Arizona (Fig. 161) .. *E. foeminalis* (Grt.) (p. 52).

26' Forewing brown or streaked with brown, almost black in some specimens from Rocky Mountain region of British Columbia and Montana 27

27 (26') Forewing, including terminal area, yellow-buff; series of black sagittate spots on proximal side of subterminal line; orbicular spot round; hind wing unevenly shaded with light and dark brown, dark median line in most specimens (Fig. 14); distributed in Great Plains of Alberta and Montana (Fig. 161) ....
.... *E. clausa* McD. (p. 57).

27' Forewing brown in most specimens; if light buff, then terminal area of forewing dark brown with dark streaks on proximal side of subterminal line; orbicular spot oval in most specimens; hind wing evenly colored, slightly lighter toward base (Figs. 7-12); widely distributed (Fig. 160) .... *E.* idahoensis (Grt.) (p. 54).

28 (23') Hind wing mottled gray-brown with median line on ventral surface; forewing with inconspicuous, irregular, basal dash; forewing with dark streaks extended from terminal area into subterminal area interrupted by pale subterminal line (Fig. 16) .... *E.* brevipennis (Sm.) (p. 59).

28' Hind wing evenly colored, pale gray-brown, slightly lighter at base, without trace of median line on ventral surface; forewing with conspicuous basal dash extended to transverse anterior line; forewing with dark streaks extended uninterrupted from terminal area into subterminal area, subterminal line not evident (Fig. 50) .... *E.* laetificans (Sm.) (p. 101).

29 (22') Forewing marked with silver-gray; inner edge of terminal area with W-mark where pale-lined veins Cu_1 and M_3 project into it (Fig. 16)......................... .... *E.* brevipennis (Sm. (p. 59).

29' Forewing brown or gray, without silver-gray streaks; inner edge of terminal area without W-mark, veins Cu_1 and

M_3 not pale-lined 30

30 (29') Forewing with median area pale gray-brown, basal and subterminal areas pale gray (Fig. 47) .... *E. dodi* McD. (p. 97).

Forewing with median and terminal areas dark brown, basal and subterminal areas paler brown with copper suffusion (Fig. 48) .... *E. infracta* (Morr.) (p. 99).

3.4. Species of the Euxoa detersa group

3.4.1. Euxoa costata (Grote)

Figs. 1, 2, 65, 96, 126, 158, 188

Agrotis costata Grote, 1876, p. 80; Vancouver Island, B.C.

Rhynchagrotis costata; Smith, 1890b, p. 38; redescription.

Rhynchagrotis costata; Smith, 1893, p. 55.

Triphaena costata; Hampson, 1903, p. 631.

Euxoa costata; Barnes and McDunnough, 1917, p. 43.

Euxoa costata; Draudt, 1924, p. 48; redescription.

Description. Vestiture of head and thorax and ground color of forewing reddish brown. Transverse lines obscure. Reniform and orbicular spots and costa shaded with silver-gray. Hind wing smoky-brown.

Expanse: 36.1±1.3 mm. Length of forewing: 17.0±0.8 mm (50 specimens).

Male genitalia (Fig. 65). Sacculus extensions slightly longer than harpes and about as stout. Sub-basal diverticulum of vesica large; median diverticulum positioned about 1/3 of distance from sub-basal bend in vesica to apex. Vesica projected to right apically.

Length of right sacculus extension: 1.71±0.08 mm (6 specimens).

Length of left sacculus extension: 1.62±0.08 mm (7 specimens).

Length of right harpe: 1.61±0.04 mm (7 specimens).

Length of right sacculus: 1.52±0.09 mm (7 specimens).

Female genitalia (Figs. 96, 126). Ductus bursae entering corpus bursae 1/3-1/2 way along right side from posterior end. Ovipositor valves with short, conical setae near apex. Ovipositor valve rounded or somewhat truncate apically.

Type material. The holotype of *Agrotis costata* Grote is a female in the collection of the British Museum (Natural History). The specimen has been dissected.

Distribution and period of flight. *Euxoa costata* occurs from southern British Columbia southward in the Cascades and Sierra Nevada Mountains to southern California (Fig. 158). Fifty-eight specimens from 21 localities were examined.

Specimens have been collected from mid-July until early September.

Habitat. This species inhabits dry conifer forests, especially those dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco).

Remarks. Male specimens of *E. costata* may be distinguished from those of other similar species by the longer sacculus extensions and harpes of the male genitalia. In external appearance, specimens of *E. costata* are most easily confused with those of *E. castanea*; for distinguishing characters see discussion under that species.

3.4.2. *Euxoa castanea* Lafontaine, new species

Figs. 3, 4, 66, 97, 127, 159, 188

Description. Antenna of male biserrate and bifasciculate. Antenna of female filiform. Frontal tubercle present. Vestiture of head and thorax dark reddish brown.

Forewing ground color chestnut brown dusted with black. Transverse anterior and posterior lines indistinct in most specimens. Subterminal area slightly paler than median area in most specimens. Terminal area dark gray-brown. Costa, reniform spot, and orbicular spot paler than median area, shaded with buff or silver-gray. Orbicular spot oval in most specimens. Area between reniform and orbicular spots, and proximal to orbicular spot, black in most specimens. Cubital vein pale and contrasting from wing base to reniform spot. Basal dash and claviform spot black.

Hind wing of both male and female gray-brown; discal spot present.

Expanse: 36.4±1.6 mm. Length of forewing: 16.8±0.7 mm (100 specimens).

Male genitalia (Fig. 66). Differing from those of *E. costata* only in proportion. Harpe and sacculus extension in males of *E. castanea* shorter than those of *E. costata* males.

Length of right sacculus extension: 1.33±0.10 mm (25 specimens).

Length of left sacculus extension: 1.24±0.10 mm (25 specimens).

Length of right harpe: 1.28±0.06 mm (25 specimens).

Length of right sacculus: 1.35±0.07 mm (25 specimens).

Female genitalia (Figs. 97, 127). Ovipositor valve triangular in outline, pointed apically. Small flange-like projection on ovipositor valve of female specimens from southern Rocky Mountains in Colorado and New Mexico.

Type material. Holotype male: Golden, B.C., 2 mi E., 3000 ft, 21 July 1960 (D.F. Hardwick), Type No. 15939 in the Canadian National Collection, Ottawa. Paratypes: 78 males, 49 females: ALBERTA: Banff, 30 July-7 Aug. 1922 (C.B.D. Garrett); Exshaw, 5 mi NE., 4225 ft, 18 July 1961 (D.F. Hardwick); Horseshoe Canyon, Drumheller, 2750 ft, 17 July 1960 (D.F. Hardwick); Lake Louise, 4 mi SE., 6000 ft, 20 July 1960 (D.F. Hardwick); Nordegg, 17 July-8 Aug. 1921 (J. McDunnough). BRITISH COLUMBIA: Crow's Nest, 5 mi NW., 4300 ft, 26 July 1960 (D.F. Hardwick); Fernie, 11 mi NE., 3600 ft, 27 July 1960 (D.F. Hardwick); Golden, 2 mi E., 3000 ft, 21 July 1960 (D.F. Hardwick); Radium Hot Springs, 16 mi N., 2900 ft, 22 July 1960 (D.F. Hardwick); Radium Hot Springs, 28 mi S., 23 July 1960 (D.F. Hardwick).

Distribution and flight period. *Euxoa castanea* occurs across the aspen parkland and southern boreal forest of western Canada, southward in the Rocky Mountains to New Mexico. It occurs in the northern Great Plains where suitable forested habitat is found. Approximately 700 specimens from 87 localities were examined.

Specimens were collected from early July until late August.

Habitat. This species is found most abundantly in dry conifer forests of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and lodgepole pine (*Pinus contorta* Dougl.). It is also found in spruce and aspen forests, particularly in the northeastern portion of its range.

Remarks. Specimens of *E. castanea* may be distinguished from those of *E. costata* and *E. idahoensis* by the dark chestnut-brown coloration of the forewing, and from the former by the pale cubital vein. In specimens of *E. costata* the forewing is light reddish brown without dark dusting; the cubital vein is not pale. Specimens of *E. idahoensis* have gray or brown forewings; the cubital vein is pale in many specimens.

3.4.3. *Euxoa foeminalis* (Smith)

Figs. 5, 6, 67, 98, 128, 161, 189

Carneades foeminalis Smith, 1900, p. 454; Colorado.

Paragrotis foeminalis; Dyar, 1902, p. 148.

Euxoa foeminalis; Hampson, 1903, p. 296.

Euxoa foeminalis; Draudt, 1924, p. 48; redescription.

Carneades foeminalis; Rindge, 1955, p. 112; type material.

Description. Vestiture of head and thorax black and gray. Ground color of forewing dark silver-gray dusted with black. Transverse lines obscure. Subterminal area, costa, reniform spot, and orbicular spot pale silver-gray, contrasted with darker ground color of remainder of forewing. Cubital vein not pale-lined. Hind wing smoky-brown.

Expanse: 36.4±1.4 mm. Length of forewing: 16.9±0.9 mm (40 specimens).

Male genitalia (Fig. 67). Indistinguishable from those of *E. idahoensis*.

Length of right sacculus extension: 1.51±0.07 mm (20 specimens).

Length of left sacculus extension: 1.45±0.08 mm (20 specimens).

Length of right harpe: 1.39±0.04 mm (20 specimens).

Length of right sacculus: 1.49±0.05 mm (20 specimens).

Female genitalia (Figs. 98, 128). Ovipositor valves more broadly rounded than those of *E. idahoensis* females.

Type material. *Carneades foeminalis* was described by Smith on the basis of two nominal male (one is a female) and two female specimens from Garfield County, Colorado. The male specimen is in the collection of the American Museum of Natural History, New York; three female specimens are in the collection of the United States National Museum (type No. 4784). A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa foeminalis* occurs in southwestern United States from north-central Utah and western Colorado southward to northern New Mexico and Arizona (Fig. 161). Forty specimens were examined from 6 localities.

Specimens have been collected from late May until mid-July.

Habitat. The habitat of this species is inferred from relatively few localities to be conifer forests. This species, however, was collected at one locality in an open oak-pine forest.

Remarks. *Euxoa foeminalis* specimens resemble dark specimens of *E. idahoensis* from montane areas of British Columbia and Montana; they differ from these in that the forewing is shaded with black rather than dark brown and the costa, reniform spot, orbicular spot, and subterminal area are all shaded with silver-gray, the cubital vein is not pale. In dark specimens of *E. idahoensis* the subterminal area is not pale, the cubital vein is pale in most specimens (compare Figs. 5 and 10). Specimens of *E. idahoensis* from the area of sympatry with *E. foeminalis* are shaded with pale brown and the cubital vein is pale in most specimens.

3.4.4. *Euxoa idahoensis* (Grote)

Figs. 7, 8, 9, 10, 11, 12, 68, 99, 129, 130, 160, 189

Agrotis idahoensis Grote, 1878, p. 171; Idaho.

Carneades idahoensis; Smith, 1890b, p. 197; redescription.

Carneades idahoensis; Smith, 1893, p. 105; catalogue.

Paragrotis idahoensis; Dyar, 1902, p. 148.

Euxoa idahoensis; Hampson, 1903, p. 295.

Euxoa costata idahoensis; Barnes and McDunnough, 1917, p. 43.

Euxoa costata form *idahoensis*; Draudt, 1924, p. 48.

Euxoa costata idahoensis; McDunnough, 1938, p. 60.

Agrotis furtivus Smith, 1890a, p. 56; California.

Carneades furtivus; Smith, 1890b, p. 197.

Carneades furtivus; Smith, 1893, p. 105; catalogue.

Paragrotis furtivus; Dyar, 1902, p. 148.

Euxoa furtiva; Hampson, 1903, p. 297.

Euxoa furtiva; Barnes and McDunnough, 1917, p. 43; = *E. costata idahoensis*.

Euxoa furtiva; Draudt, 1924, p. 48; = *E. costata* form *idahoensis*.

Description. Vestiture of head and thorax gray-brown. Color and markings of forewing extremely variable; most common and widespread form (Figs. 7, 8) with forewing pale brown with dark brown streaks. Terminal space and sagittate spots proximal to subterminal line dark gray-brown. Costa, reniform spot, orbicular spot, and cubital vein paler than remainder of forewing. Orbicular spot oblong in most specimens.

Specimens from Great Plains region pale gray (Fig. 9), those from montane areas of British Columbia and Montana dark brown (Fig. 10). Some specimens from Black Hills, South Dakota, and from montane areas of Colorado heavily streaked (Fig. 12) and resembling specimens of *E. oblongistigma*. Many specimens from northern Great Basin without pale costa (Fig. 11) and frequently without pale-filled spots.

Hind wing smoky-brown, paler toward base; discal spot present.

Expanse: 36.2±1.7 mm. Length of forewing: 16.3±0.8 mm (100 specimens).

Male genitalia (Fig. 68). Indistinguishable from those of *E. castanea*, *E. foeminalis*, and *E. clausa*.

Length of right sacculus extension: 1.42±0.09 mm (30 specimens).

Length of left sacculus extension: 1.33±0.09 mm (30 specimens).

Length of right harpe: 1.39±0.06 mm (30 specimens).

Length of right sacculus: 1.37±0.07 mm (30 specimens).

Female genitalia (Figs. 99, 129, 130). Ovipositor valve of females from northern and western portion of range rounded apically (Fig. 129), those of females from Wyoming Basin and southern Rocky Mountains more acutely angled, small flange-like projection in some specimens (Fig. 130).

Type material. The holotype of *Agrotis idahoensis* is a male in the collection of the British Museum (Natural History) from Idaho. *Agrotis furtivus* was described by Smith on the basis of three nominal females (one specimen is a male) from California. A lectotype will be designated by Todd (1980) from the syntypes in the collection of the United States National Museum.

Distribution and period of flight. Euxoa idahoensis is found in western North America as far east as south-central Saskatchewan and western South Dakota. Approximately 600 specimens were examined from 96 localities.

Adults have been collected from mid-June until late August, however, most were collected in the latter half of July.

Habitat. Although this species is most common in dry conifer forests of pine, fir, and Douglas-fir, it is also found occasionally in piñon-juniper woodland in the Great Basin, and in deciduous thickets in the Great Plains.

Remarks. Euxoa idahoensis is probably the most variable species of any in the E. detersa group with numerous color forms occurring in different parts of its range. The most widespread form (Figs. 7 and 8) grades imperceptibly into the other more localized geographic forms where they occur together.

Specimens of Euxoa idahoensis cannot be distinguished from those of the other members of the E. costata-E. foeminalis-E. clausa series by structural characters. They can be distinguished from specimens of these species by characters in key.

3.4.5. *Euxoa clausa* McDunnough

Figs. 13, 14, 69, 100, 131, 161, 189

Euxoa clausa McDunnough, 1923, p. 163; Lethbridge, Alberta.

Euxoa costata form *clausa*; Draudt, 1924, p. 48.

Euxoa clausa; McDunnough, 1938, p. 61.

Description. Male antenna markedly biserrate, serrations deeper than those of *E. idahoensis* males. Vestiture of head and thorax light yellowish brown. Ground color of forewing pale yellow-brown overlaid with dusting of brown scales. Transverse lines present in most specimens but obscure. Terminal area concolorous or slightly darker than remainder of forewing. Subterminal area with series of black sagittate spots on proximal side of subterminal line in most specimens (Fig. 14). Costa, orbicular spot, and reniform spot not particularly pale. Hind wing unevenly colored with smoky-brown shading on outer third of wing, on median line, and on discal spot.

Expanse: 34.9±2.3 mm. Length of forewing: 15.8±1.0 mm (40 specimens).

Male genitalia (Fig. 69). Indistinguishable from those of *E. idahoensis* males.

Length of right sacculus extension: 1.40±0.09 mm (20 specimens).

Length of left sacculus extension: 1.33±0.08 mm (20 specimens).

Length of right harpe: 1.43±0.06 mm (20 specimens).

Length of right sacculus: 1.40±0.05 mm (20 specimens).

Female genitalia (Figs. 100, 131). Indistinguishable from those of E. idahoensis.

Type material. The holotype of E. clausa is a male from Lethbridge, Alberta, type No. 598 in the Canadian National Collection, Ottawa. The specimen has not been dissected.

Distribution and period of flight. Specimens of E. clausa have been collected only in the northwestern Great Plains (Fig. 161). Fifty specimens from 6 localities were examined; these were collected from mid-July until mid-August.

Habitat. From limited available data, it appears that this species inhabits open shortgrass prairie.

Remarks. Euxoa clausa occurs sympatrically with a pale form of E. idahoensis (Fig. 9) in the northern Great Plains. Specimens of these two species may be distinguished by characters in key.

3.4.6. Euxoa brevipennis (Smith)

Figs. 15, 16, 70, 101, 132, 168

Agrotis brevipennis Smith, 1887, p. 455; California, Colorado, Nevada.

Carneades brevipennis; Smith, 1890b, p. 140; redescription.

Carneades brevipennis; Smith, 1893, p. 89; catalogue.

Paragrotis brevipennis; Dyar, 1902, p. 140.

Euxoa brevipennis; Hampson, 1903, p. 208.

Euxoa brevistriga Smith, 1910b, p. 257; Colorado, probably Denver.

Euxoa brevipennis brevistriga; Barnes and McDunnough, 1917, p. 41.

Euxoa brevipennis form brevistriga; Draudt, 1924, p. 37.

Euxoa brevistriga; Rindge, 1955, p. 103; type material.

Euxoa angulirena Smith, 1910b, p. 257; Colorado.

Euxoa brevipennis ab. angulirena; Barnes and McDunnough, 1917, p. 41.

Euxoa angulirena; Rindge, 1955, p. 101; type material.

Description. Vestiture of head and thorax gray, or mixture gray and black scales. Ground color of forewing gray, streaked longitudinally with white and dark gray in most specimens; some specimens with little or no pale streaking. Transverse anterior and posterior lines barely evident or absent. Subterminal area and posterior half of median area streaked in most specimens with veins dark, interveinal area pale. Terminal area dark gray, its inner margin streaked into subterminal area; streaks interrupted by pale subterminal line in many specimens. Dark terminal shade indented by pale W-mark where pale-lined veins Cu_1 and M_3 project into it. Costa pale in most specimens. Reniform and orbicular spots with pale line between black outline and gray-filled center. Black, basal dash in some specimens. Hind wing of male white with narrow gray terminal line and in some specimens on veins as well. Hind wing of female pale gray with dusting of darker gray scales on outer third of wing, on median line, and on veins.

Expanse: 35.1±1.5 mm. Length of forewing: 17.1±0.8 mm (100 specimens).

Male genitalia (Fig. 70). Distinguishable from those of other species in *E. detersa* group by characters of vesica. Vesica with bend, or slight twist in it before it bends to project dorsally. Sub-basal diverticulum curved to left apically. Sacculus extension not straight or incurved as are those of most other species but slightly S-curved, bent away from cucullus near apex. Sacculus extensions stouter than those of males of *E. costata*-*E. foeminalis*-*E. clausa* series.

Length of right sacculus extension: 1.45±0.10 mm (20 specimens).

Length of left sacculus extension: 1.39±0.10 mm (20 specimens).

Length of right harpe: 1.25±0.06 mm (20 specimens).

Length of right sacculus: 1.42±0.06 mm (20 specimens).

Female genitalia (Figs. 101, 132). Similar to those of *E. dodi* (Fig. 115) and *E. infracta* (Fig. 116) but corpus bursae slightly constricted mesially in most females of *E. brevipennis*.

Type material. It is not known how many specimens Smith based *Agrotis brevipennis* on. The only type material located is two specimens in the collection of the United States National Museum.

One of these will be selected as lectotype by Todd (1980).

Smith described *Euxoa brevistriga* from two males collected in Colorado (probably near Denver according to Smith). One of these males, in the collection of the American Museum of Natural History, will be selected as lectotype by Todd (1980).

The holotype of *Euxoa angulirena* Smith is a female from Colorado in the collection of the American Museum of Natural History. The specimen has been dissected.

Distribution and period of flight. *Euxoa brevipennis* occurs throughout the intermontane region and in the western Great Plains (Fig. 168). Approximately 350 specimens from 53 localities were examined.

This is a late-flying species; adults have been collected from early September until late October in the north and November in the south.

Habitat. This species inhabits dry, open sagebrush areas; it also occurs in open piñon-juniper woodland where sagebrush is abundant.

Remarks. A combination of large size, pattern of forewing streaking, lack of transverse lines, and pale hind wing allow specimens of *E. brevipennis* to be distinguished from those of other species in the *E. detersa* group. The larva has been reared on tumblemustard (*Sisymbrium* spp.), hare's-ear mustard (*Conringia orientalis* (L.) Dumort), Russian thistle (*Salsola kali* L.) and sweet clover (*Melilotus* spp.) in Montana (Cook, 1930b).

3.4.7. *Euxoa servita* (Smith)

Figs. 17, 18, 19, 71, 102, 133, 162

Carneades servitus Smith, 1895, p. 336; Colorado; Calgary, Alberta.

Paragrotis servitus; Dyar, 1902, p. 148.

Euxoa servita; Hampson, 1903, p. 308.

Euxoa servita; Dod, 1905, p. 148; probably aberration of *E. redimicula*.

Euxoa redimicula ab. *servita*; Barnes and McDunnough, 1917, p. 43.

Euxoa servita; McDunnough, 1949, p. 5; good species.

Euxoa servita; McDunnough, 1950, p. 391; bibliography.

Agrotis servita; Forbes, 1954, p. 42.

Carneades servitus; Rindge, 1955, p. 130; type material.

Euxoa servita; Lafontaine, 1974a, p. 409; redescription.

Euxoa servita novangliae McDunnough, 1950, p. 391; Franconia, New Hampshire.

Description. Vestiture of head and thorax gray. Dorsal half of prothoracic collar reddish brown or gray. Ground color of forewing various shades of gray or brownish gray, darker in specimens from forested areas. Maculation complete but appearing streaked and blurred in most specimens. Transverse posterior line slightly scalloped between veins, series of small, dark, sagittate spots on proximal side extended into median area. Terminal area dark gray, its inner margin streaked into subterminal area. Several small, black streaks extended from terminal area into subterminal area opposite reniform spot. Hind wing of both sexes smoky-brown.

Expanse: 31.4±1.9 mm. Length of forewing: 15.4±0.7 mm (100 specimens).

Male genitalia (Fig. 71). Distinguishable from those of *E. redimicula*, *E. auripennis*, and *E. arizonensis* only by numerical methods (see Lafontaine, 1974a).

Length of right sacculus extension: 1.51±0.09 mm (40 specimens).

Length of left sacculus extension: 1.41±0.11 mm (40 specimens).

Length of right harpe: 1.24±0.06 mm (40 specimens).

Length of right sacculus: 1.39±0.06 mm (40 specimens).

Female genitalia (Figs. 102, 133). Distinguishable from those of other three members of *E. servita*-*E. arizonensis* series by form of ovipositor valve. Apical third of ovipositor valve clothed with stout setae, appearing mace-like; those of other species of series clothed with fine setae, sclerotized flange-like projection at apex of each valve.

Type material. *Carneades servitus* was described by Smith from two specimens: a male from Colorado in the collection of the American Museum of Natural History, New York; a female from Calgary, Alberta, in the collection of the United States National Museum. A lectotype will be designated by Todd (1980).

The holotype of *Euxoa servita novangliae* is a female from Franconia, New Hampshire in the collection of the American Museum of Natural History. The specimen has been dissected.

Distribution and period of flight. *Euxoa servita* occurs from Nova Scotia westward across southern Canada and northern United States to British Columbia and southward in the Rocky Mountain region to central Arizona and New Mexico (Fig. 162). It has not been collected in the Cascades or Sierra Nevada Mountains. Approximately 1000 specimens from 147 localities were examined.

Adults have been collected from mid-July until late August.

Habitat. East of the Rocky Mountains this species inhabits forested areas dominated by spruce and aspen. In British Columbia and in the Rocky Mountain region it is found in aspen and Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco) forests, and more uncommonly, in areas dominated by lodgepole pine (Pinus contorta Dougl.) and ponderosa pine (Pinus ponderosa Dougl.). In general, this species is found in more mesic habitats than E. redimicula, E. auripennis, and E. arizonensis occur in.

Remarks. Female specimens of E. servita are easily distinguished from those of E. redimicula, E. auripennis, and E. arizonensis by the stout setae rather than apical flange-like projection on the ovipositor valve. Separation of males of the four species was discussed by Lafontaine (1974a). Most male specimens can be distinguished by characters in key. Euxoa servita adults have an earlier flight period than do those of the other three species, however, there is usually some overlap.

The subspecific name novangliae McDunnough has been used for dark brown specimens from populations in eastern North America. I do not consider eastern populations to be subspecifically distinct because dark brown forms also occur in mesic conifer forest areas in western North America. Darker wing color appears to be associated with more mesic habitats.

3.4.8. *Euxoa redimicula* (Morrison)

Figs. 20, 21, 72, 103, 134, 163, 190

Agrotis redimacula Morrison, 1874, p. 165; Colorado, New York, Massachusetts.

Agrotis redimicula; Morrison, 1875b, p. 57; spelling correction.

Carneades redimicula; Smith, 1890b, p. 202; redescription.

Carneades redimicula; Smith, 1893, p. 107; catalogue.

Paragrotis redimicula; Dyar, 1902, p. 148.

Euxoa redimicula; Hampson, 1903, p. 306.

Euxoa redimicula; McDunnough, 1949, p. 5; type limitation.

Euxoa redimicula; McDunnough, 1950, p. 390; bibliography.

Agrotis redimicula; Forbes, 1954, p. 42; redescription.

Euxoa redimicula; Lafontaine, 1974a, p. 412; redescription; lectotype selection.

Agrotis redimicula; Lafontaine, 1979; correction of original spelling.

Description. Vestiture of head and thorax gray-brown. Upper half of prothoracic collar gray or reddish brown. Ground color of forewing pale brown or brownish-gray. Transverse lines present but obscure in most specimens. Basal, median, and subterminal areas essentially concolorous in most specimens; subterminal area slightly paler in some specimens. Terminal area gray-brown, darker than ground color. Area between reniform and orbicular spots, and proximal to orbicular spot, black and contrasted with ground color. Claviform spot small. Hind wing of male with dark terminal band; basal two-thirds of wing pale buff, outer third smoky-brown. Hind wing of female smoky-brown to base.

Expanse: 31.6±1.8 mm. Length of forewing: 15.6±0.8 mm (60 specimens).

Male genitalia (Fig. 72). Distinguishable from those of *E. servita*, *E. auripennis* and *E. arizonensis* males only by numerical methods (see Lafontaine, 1974a).

Length of right sacculus extension: 1.39±0.13 mm (22 specimens).

Length of left sacculus extension: 1.30±0.16 mm (22 specimens).

Length of right harpe: 1.19±0.05 mm (22 specimens).

Length of right sacculus: 1.38±0.07 mm (22 specimens).

Female genitalia (Figs. 103, 134). Distinguishable from those of *E. servita* female by the presence of apical flange-like projection and from those of *E. auripennis* female by elongate finger-like flange-like projection rather than rounded, ear-like projection. Not distinguishable from those of *E. arizonensis* female although flange-like projection of *E. redimicula* female larger than that of *E. arizonensis* female (compare figures 134 and 136).

Type material. The lectotype of *Agrotis redimicula* is a female from Cambridge, Massachusetts, in the collection of Michigan State University, East Lansing. The specimen has been dissected.

Distribution and period of flight. *Euxoa redimicula* occurs from Nova Scotia southward to New Jersey and westward to western Saskatchewan, central Montana and western Wyoming. Approximately 120 specimens from 49 localities were examined.

Specimens have been collected from late July until mid-September.

Habitat. In the east, *Euxoa redimicula* inhabits dry deciduous forests. In the Great Plains, it occurs in groves of aspen, cottonwood, and ponderosa pine.

Remarks. Females of *E. redimicula* may be distinguished from those of *E. servita* and *E. auripennis* by the long, finger-like flange-like projection on the ovipositor valve and by lack of contrast between median and subterminal areas of the forewing. Males of *E. redimicula* may be distinguished by hind wing color; this is pale buff with a dark terminal band. Hind wings of males of *E. servita*, *E. auripennis*, and *E. arizonensis* are dark, slightly paler near base in many specimens.

3.4.9. *Euxoa auripennis* Lafontaine

Figs. 22, 23, 73, 104, 135, 164, 190

Euxoa auripennis Lafontaine, 1974a, p. 412; Cranbrook, B.C.

Description. Vestiture of head and basal half of prothoracic collar white; upper half of prothoracic collar reddish brown in most specimens, gray in some specimens. Vestiture of remainder of thorax gray or brown laterally, white dorsally. Ground color of forewing various shades of gray. Transverse lines prominent. Transverse posterior line scalloped between veins, black shade of teeth extended on veins in subterminal area. Basal and subterminal areas silver-gray. Median area gray-brown, contrasted with paler coloration of basal and subterminal areas. Terminal area dark gray, its inner margin not streaked into subterminal area. Reniform and orbicular spots large, pale-filled. Basal dash black, prominent. Hind wing smoky-brown, paler near base.

Expanse: 31.3±1.5 mm. Length of forewing: 15.4±0.7 mm (100 specimens).

Male genitalia (Fig. 73). Distinguishable from those of *E. servita*, *E. redimicula*, and *E. arizonensis* only by numerical methods (see Lafontaine, 1974a).

Length of right sacculus extension: 1.35±0.10 mm (34 specimens).

Length of left sacculus extension: 1.23±0.14 mm (34 specimens).

Length of right harpe: 1.12±0.04 mm (34 specimens).

Length of right sacculus: 1.30±0.05 mm (34 specimens).

Female genitalia (Figs. 104, 135). Distinguishable from those of *E. servita* female by sclerotized flange-like projection on ovipositor valve and from those of *E. redimicula* and *E. arizonensis* females by rounded, ear-like, rather than elongate, finger-like sclerotized projection.

Type material. The holotype of *E. auripennis* Lafontaine is a female (type No. 13191) in the Canadian National Collection, Ottawa.

Distribution and period of flight. *Euxoa auripennis* occurs in southern Canada and northern United States from southern Manitoba and northeastern North Dakota westward to British Columbia and Washington. In western North America it occurs southward in the Rocky Mountain region to south-central Colorado and southward in the Cascades- Sierra Nevada Mountains to southern California (Fig. 164). Approximately 400 specimens from 88 localities were examined.

Specimens have been collected from late July until late September.

Habitat. In most of its range *Euxoa auripennis* occurs in ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) parkland. In the northern Great Plains region it occurs in aspen woodland.

Remarks. Females of *Euxoa auripennis* may be distinguished from those of *E. servita*, *E. redimicula* and *E. arizonensis* by characters described above and in key. Males of *E. servita* and *E. redimicula* may be distinguished from *E. auripennis* male by wing color and maculation characters given in key; those of *E. auripennis* and *E. arizonensis* can frequently be distinguished only by numerical methods (see Lafontaine, 1974a) and by range. Where ranges of the two species overlap in southern Colorado, they are separated by habitat: *E. auripennis* occurs in more mesic habitats, such as pine forests, than does *E. arizonensis* which occurs in xeric piñon-juniper woodland. Habitat data are not available for the southern California collections of the two species.

3.4.10. *Euxoa arizonensis* Lafontaine

Figs. 24, 74, 105, 136, 164, 190

Euxoa arizonensis Lafontaine, 1974a, p. 416; White Mts., Arizona.

Description. Maculation and color almost identical to that of *E. auripennis* specimens but forewing darker in most *E. arizonensis* specimens. Basal and subterminal areas silver-gray, dusted with black scales. Median area dark gray, without pale streak distal to claviform spot in most specimens. Reniform and orbicular spots silver-gray, dusted with black scales.

Expanse: 29.5±1.9 mm. Length of forewing: 14.9±0.7 mm (40 specimens).

Male genitalia (Fig. 74). Distinguishable from those of *E. servita*, *E. redimicula*, and *E. auripennis* only by numerical methods (see Lafontaine, 1974a).

Length of right sacculus extension: 1.43±0.07 mm (25 specimens).

Length of left sacculus extension: 1.19±0.08 mm (25 specimens).

Length of right harpe: 1.06±0.04 mm (25 specimens).

Length of right sacculus: 1.28±0.05 mm (25 specimens).

Female genitalia (Figs. 105, 136). Distinguishable from those of *E. servita* female by the presence of apical flange-like projection on ovipositor valve and from those of *E. auripennis* by elongate, finger-like flange-like projection rather than rounded, ear-like projection. Indistinguishable from those of *E. redimicula* female although flange-like projection of *E. arizonensis* female smaller than that of E. redimicula female (compare figures 134 and 136).

Type material. The holotype of E. arizonensis is a female (type No. 13192) in the Canadian National Collection, Ottawa.

Distribution and period of flight. Euxoa arizonensis occurs in southwestern United States from central Colorado and western New Mexico westward to central Nevada and southern California (Fig. 164). Approximately 100 specimens from 21 localities were examined.

Specimens have been collected from early August until mid-September.

Habitat. In the southern portion of its range Euxoa arizonensis occurs in ponderosa pine (Pinus ponderosa Dougl.) parkland. In Colorado, Nevada, and possibly in California, E. arizonensis occurs in piñon-juniper woodland.

Remarks. Euxoa arizonensis is very similar to E. auripennis in both markings and structural characters (see remarks under E. auripennis) and the two species might better be treated as subspecies. They are treated as species here because differences in ovipositor valves suggests that females of the two species may oviposit in different soil types (i.e. are ecologically distinct) and differences in ovipositor valve shape are most pronounced in the area of sympatry viz. central Colorado.

3.4.11. *Euxoa olivalis* (Grote)

Figs. 25, 26, 27, 75, 106, 137, 165

Agrotis olivalis Grote, 1879, p. 43; Colorado.

Carneades olivalis; Smith, 1890b, p. 141; redescription.

Carneades olivalis; Smith, 1893, p. 89; catalogue.

Paragrotis olivalis; Dyar, 1902, p. 140.

Euxoa olivalis; Hampson, 1903, p. 211.

Euxoa olivalis; Draudt, 1924, p. 38; = *E. plagigera* (Morr.).

Euxoa mcdunnoughi Cook, 1930a, p. 147; Jefferson Co., Montana.

Euxoa mcdunnoughi; McDunnough, 1938, p. 57; = *E. olivalis*.

Description. Vestiture of head and thorax gray, brown and black scales; transverse band of white scales posterior to prothoracic collar. Ground color of forewing brown or gray, longitudinally streaked with black, pale gray, and dark brown. Transverse lines essentially absent. Terminal area slightly darker than ground color of forewing. Series of black, sagittate spots on proximal side of subterminal line in most specimens. Costa not pale, or with dark and pale lines crossing it where transverse lines would be. Color of costa separated from pale-lined cubital vein near wing base by black line. Orbicular and reniform spots outlined in white. Orbicular spot elongate and rectangular, or slightly oval, about twice as long as wide. Black basal dash thin and inconspicuous in most specimens. Hind wing of male pale buff basally with smoky-brown shading on outer quarter of wing. Hind wing of female similar to that of male, or smoky-brown to wing base.

Expanse: 31.9±1.3 mm. Length of forewing: 15.9±0.6 mm (100 specimens).

Male genitalia (Fig. 75). Distinguishable from those of E. agema and E. oblongistigma by longer sacculus extensions. Harpe pubescent.

Length of right sacculus extension: 1.57±0.07 mm (25 specimens).

Length of left sacculus extension: 1.43±0.08 mm (25 specimens).

Length of right harpe: 1.03±0.04 mm (25 specimens).

Length of right sacculus: 1.30±0.05 mm (25 specimens).

Female genitalia (Figs. 106, 137). Indistinguishable from those of E. oblongistigma and E. agema females. Those of these three species may be distinguished from those of females of other species in the E. detersa group by the rounded or pear-shaped rather than elongate corpus bursae.

Type material. The holotype of Agrotis olivalis Grote is a female in the collection of the British Museum (Natural History). The specimen has been dissected.

The holotype of Euxoa mcdunnoughi Cook is a male in the Montana Experiment Station collection, Bozeman.

Distribution and period of flight. Euxoa olivalis occurs in western North America from southern Saskatchewan westward to southern British Columbia and southward to northern New Mexico, Arizona and southern California (Fig. 165). Approximately 1100 specimens from 98 localities were examined.

Specimens have been collected from late June until early September; the flight period is later, on the average, in the south than it is in the north.

Habitat. *Euxoa olivalis* occurs in a variety of habitats. In the Great Basin it occurs in piñon-juniper woodland; in montane areas it occurs in open ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) parkland; in the Great Plains it has been collected in sagebrush areas. In general, *E. olivalis* is found in habitats intermediate between xeric habitats of *E. oblongistigma* and mesic ones of *E. agema*.

Remarks. Most specimens of *E. olivalis* may be distinguished from those of *E. oblongistigma* and *E. agema* by characters in key. Specimens from populations of *E. olivalis* from more mesic, higher elevation, localities are darker and have more brown coloration than do specimens from more xeric, lower elevation, localities and are similar in color and pattern to *E. agema* specimens. Although males of the two species may be distinguished by characters of the genitalia, females from more mesic localities can sometimes only be identified by association with males.

3.4.12. Euxoa agema (Strecker)

Figs. 28, 29, 76, 138, 166, 191

Agrotis agema Strecker, 1899, p. 5; Colorado.

Paragrotis agema; Dyar, 1902, p. 140.

Euxoa agema; Hampson, 1903, p. 666.

Euxoa agema; Barnes and McDunnough, 1917, p. 41; = E. oblongistigma.

Description. Head, thorax, and pattern of forewing similar to that of E. olivalis specimens. Ground color of forewing dark brown longitudinally streaked with light brown; forewing darker and without gray streaks of most specimens of E. olivalis. Hind wing smoky-brown, slightly paler toward base.

Expanse: 32.4±1.2 mm. Length of forewing: 15.8±0.7 mm (100 specimens).

Male genitalia (Fig. 76). Distinguishable from those of E. olivalis male by shorter sacculus extensions. In male of E. agema sacculus extensions appear to be about as long as harpes; in male of E. olivalis they are markedly longer than harpes. Male genitalia of E. agema indistinguishable from those of E. oblongistigma male.

Length of right sacculus extension: 1.19±0.06 mm (25 specimens).

Length of left sacculus extension: 1.08±0.07 mm (25 specimens).

Length of right harpe: 1.13±0.06 mm (25 specimens).

Length of right sacculus: 1.26±0.05 mm (25 specimens).

Female genitalia (Figs. 107, 138). Indistinguishable from those of E. olivalis, and E. oblongistigma females.

Type material. The holotype of *Agrotis agema* Strecker is a female in the collection of the Field Museum of Natural History, Chicago.

Distribution and period of flight. *Euxoa agema* occurs in mountain ranges that surround the Great Basin and Colorado Plateau (Fig. 166). Within the Great Basin it has been collected only in the Ruby Mountains, Nevada. Approximately 350 specimens from 38 localities have been examined.

Adults have been collected from mid-July until early September.

Habitat. This species inhabits forested areas of spruce, aspen, and lodgepole pine (*Pinus contorta* Dougl.). Although specimens of *E. agema* are sometimes collected with those of *E. olivalis* and *E. oblongistigma*, they are generally found in more mesic habitats than are those of the other two species.

Remarks. Specimens of *E. agema* may be distinguished from those of *E. olivalis* and *E. oblongistigma* by characters in key (also see remarks under *E. olivalis*).

3.4.13. Euxoa oblongistigma (Smith)

Figs. 30, 31, 32, 77, 108, 139, 167, 191

Agrotis oblongistigma Smith, 1887, p. 454; Montana, Black Hills, South Dakota.

Carneades oblongistigma; Smith, 1890b, p. 140; redescription.

Carneades oblongistigma; Smith, 1893, p. 89; catalogue.

Paragrotis oblongistigma; Dyar, 1902, p. 140.

Euxoa oblongistigma; Hampson, 1903, p. 210.

Euxoa oblongistigma; Draudt, 1924, p. 38; redescription.

Description. Vestiture of head and thorax brown and black scales; transverse band of white scales posterior to prothoracic collar in some specimens. Ground color of forewing buff or pale gray streaked longitudinally with dark brown and black. Transverse lines essentially absent. Terminal area slightly darker than remainder of forewing. Series of black, sagittate spots on proximal side of subterminal line in most specimens. Costa pale, evenly colored, without cross-lines; pale color of costa extended to cubital vein near wing base, not separated from it by black line. Reniform and orbicular spots pale, without white line between center of spot and black outline. Orbicular spot elongate and rectangular or slightly oval, about twice as long as wide. Black basal dash prominent in most specimens. Hind wing of male pale buff, darker smoky-brown terminal band present in many specimens. Hind wing of female similar to that of male but smoky-brown shading more extensive.

Expanse: 32.0±1.2 mm. Length of forewing: 15.7±0.8 mm (100 specimens).

Male genitalia (Fig. 77). Indistinguishable from those of *E. agema* male. Distinguishable from those of *E. olivalis* male by shorter sacculus extensions.

Length of right sacculus extension: 1.32±0.07 mm (25 specimens).

Length of left sacculus extension: 1.19±0.10 mm (25 specimens).

Length of right harpe: 1.15±0.06 mm (25 specimens).

Length of right sacculus: 1.28±0.07 mm (25 specimens).

Female genitalia (Figs. 108, 139). Indistinguishable from those of *E. olivalis* and *E. agema* females.

Type material. *Agrotis oblongistigma* was described by Smith from four female specimens from Montana and South Dakota. Only two of these specimens have been located, these in the collection of the United States National Museum. One of these will be selected as lectotype by Todd (1980).

Distribution and period of flight. *Euxoa oblongistigma* occurs in the western Great Plains from southern Saskatchewan and Alberta southward to northern Colorado, and in the intermontane region from southern British Columbia southward to northern New Mexico, southern Utah, central Nevada, and central California (Fig. 167). Approximately 700 specimens from 75 localities were examined.

Habitat. *Euxoa oblongistigma* inhabits dry, sagebrush areas and open conifer woods where sagebrush is plentiful.

Remarks. Specimens of *E. oblongistigma* may be distinguished from those of *E. olivalis* and *E. agema* by characters in key.

Generally, the pale, evenly colored costa, reniform spot and orbicular spot allow specimens of *E. oblongistigma* to be readily distinguished from those of the other two species.

3.4.14. Euxoa citricolor (Grote)

Figs. 33. 34, 35, 78, 109, 140, 169, 192

Agrotis citricolor Grote, 1880b, p. 154; Colorado.

Carneades citricolor; Grote, 1883, p. 26.

Carneades citricolor; Smith, 1890b, p. 155; redescription.

Carneades citricolor; Smith, 1893, p. 92; catalogue.

Paragrotis citricolor; Dyar, 1902, p. 142.

Euxoa citricolor; Draudt, 1924, p. 39; redescription.

Euxoa citricolor ab. postmedialis Strand, 1915, p. 144; Prescott, Arizona; infrasubspecific name.

Euxoa citricolor form postmedialis Draudt, 1924, p. 39; validation of name.

Euxoa citricolor ab. postmedialis; McDunnough, 1938; checklist.

Description. Vestiture of head and thorax yellow. Ground color of forewing yellow, overlaid with dusting of brown scales in many specimens. Transverse lines obscure or absent. Terminal space, reniform spot, and in many specimens orbicular spot, dark gray-brown, contrasting. Hind wing white in most specimens, a few specimens with some dark shading on outer third of wing or along veins.

Expanse: 35.3±1.3 mm. Length of forewing: 16.8±0.8 mm (100 specimens).

Male genitalia (Fig. 78). Distinguishable from those of E. tronella by shape of harpe and sacculus extension, and by smaller sub-basal diverticulum of vesica. In specimens of E. citricolor, harpe and sacculus not markedly curved near base but appear slightly squeezed together; in specimens of E. tronella, harpe and sacculus extension markedly curved near base, an even C-shape, or 'U', where they meet.

Length of right sacculus extension: 1.78±0.10 mm (22 specimens).

Length of left sacculus extension: 1.78±0.11 mm (22 specimens).

Length of right harpe: 1.32±0.06 mm (22 specimens).

Length of right sacculus: 1.48±0.07 mm (22 specimens).

Female genitalia (Figs. 109, 140). Indistinguishable from those of E. tronella female. The genitalia of these two species distinguishable from those of other species in E. detersa group by characters in key.

Type material. Grote described A. citricolor on the basis of two specimens, a male and a female. Only the male has been located, this in the collection of the British Museum (Natural History). This specimen is here designated lectotype. The specimen, a male in good condition, is labelled "Colorado, Grote Coll., 81-116", "type". A genitalic slide has been prepared (No. 6330). The holotype of E. postmedialis Draudt is in the collection of the British Museum (Natural History). The specimen, a female from Prescott, Arizona, has been dissected.

Distribution and period of flight. Euxoa citricolor occurs from southern Washington southward to southern California and eastward to central Wyoming, Colorado and New Mexico. It has also been collected in the northern Great Plains at Watford City, North

Dakota, and at Mitchell, South Dakota (see figure 169). Approximately 400 specimens from 72 localities were examined.

Specimens have been collected from late August until early October.

Habitat. This species inhabits open aridlands where the flora is dominated by big sagebrush (*Artemisia tridentata* Nutt.). It is most common in areas where the soil is loose and coarse. In the Great Plains it has been collected in areas of extensive erosion such as badlands and river terraces.

Remarks. Specimens of *E. citricolor* may be distinguished from those of *E. tronella* by the color of the forewing, as well as by differences in male genitalia given above. In specimens of *E. citricolor*, the forewing is yellow; in those of *E. tronella*, the forewing is cream-colored, or pale buff, with a dusting of darker scales.

3.4.15. *Euxoa tronella* (Smith)

Figs. 36, 37, 38, 79, 110, 141, 170, 192

Carneades tronellus Smith, 1903a, p. 11; Stockton, Utah.

Euxoa tronella; Hampson, 1903, p. 432.

Euxoa tronellus; Barnes and McDunnough, 1917, p. 41; = *E. citricolor*.

Euxoa tronellus; Draudt, 1924, p. 39; = *E. citricolor*.

Carneades tronellus; Rindge, 1955, p. 134; type material.

Description. Vestiture of head and thorax cream-colored or pale, buffy gray. Ground color of forewing cream-colored or pale buff, dusted with darker scales in most specimens. Transverse lines obscure or absent. Terminal area gray, darker than ground color in most specimens. Reniform and orbicular spots partially filled with gray shading or concolorous with ground color. Hind wing white in most specimens; smoky-brown shading on terminal margin of wing and on median line in some specimens.

Some geographical variation evident. Specimens from Mojave Desert, California, cream-colored, without darker scales or maculation. Specimens from Saskatchewan and North Dakota buff-colored, heavily dusted with dark scales; hind wing with terminal half shaded with smoky-brown. Specimens from Great Basin and Wyoming fall in between these extremes in an east-west cline.

Expanse: 34.0±1.7 mm. Length of forewing: 16.0±0.6 mm (100 specimens).

Male genitalia (Fig. 79). Distinguishable from those of

E. citricolor male by shape of harpe and sacculus extension, and by larger sub-basal diverticulum of vesica. In male of *E. tronella*, harpe and sacculus extension markedly curved near base, an even C-shape, or 'U' formed where they meet; in male of *E. citricolor*, harpe and sacculus extension not markedly curved near base but appear slightly squeezed together.

Length of right sacculus extension: 1.61±0.10 mm (20 specimens).

Length of left sacculus extension: 1.60±0.09 mm (20 specimens).

Length of right harpe: 1.30±0.07 mm (20 specimens).

Length of right sacculus: 1.37±0.07 mm (20 specimens).

Female genitalia (Figs. 110, 141). Indistinguishable from those of *E. citricolor* female.

Type material. *Carneades tronellus* was described by Smith on the basis of six specimens from Stockton, Utah. Of these six, only three specimens have been located, a male in the collection of the American Museum of Natural History, and a male and female in the collection of the United States National Museum. A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa tronella* occurs in the western Great Plains from southern Saskatchewan and Alberta southward to western South Dakota and southern Wyoming, and in the intermontane region from southern Washington southward to northern New Mexico and southern California (Fig. 170). Approximately 600 specimens from 53 localities were examined.

Specimens have been collected from late August until early October.

Habitat. *Euxoa tronella* inhabits open aridlands where big sagebrush (*Artemisia tridentata* Nutt.) is abundant. This species is apparently similar to *E. citricolor* in habitat requirements in the intermontane region; specimens of the two species are frequently collected together. In the Great Plains, *E. tronella* is not restricted to areas of extensive erosion as is *E. citricolor*.

Remarks. Specimens of *E. tronella* may be distinguished from those of *E. citricolor* by forewing color, and by differences in male genitalia as given under *E. citricolor*.

3.4.16. *Euxoa teleboa* (Smith)

Figs. 39, 40, 80, 111, 142, 171

Carneades teleboa Smith, 1890b, p. 219; Las Vegas, New Mexico.

Carneades teleboa; Smith, 1893, p. 99; catalogue.

Paragrotis teleboa; Dyar, 1902, p. 145.

Euxoa teleboa; Hampson, 1903, p. 261.

Euxoa teleboa; Draudt, 1924, p. 45; redescription.

Carneades pedalis Smith, 1890b, p. 220; Colorado.

Carneades pedalis; Smith, 1893, p. 98; catalogue.

Paragrotis pedalis; Dyar, 1902, p. 145.

Euxoa pedalis; Hampson, 1903, p. 261.

Euxoa pedalis; Draudt, 1924, p. 45; redescription.

Euxoa pedalis; Lafontaine, 1980; = *E. teleboa*.

Carneades recticincta Smith, 1895, p. 334; Calgary, Alberta.

Paragrotis recticincta; Dyar, 1902, p. 145.

Euxoa recticincta; Hampson, 1903, p. 261.

Euxoa recticincta; Draudt, 1924, p. 45; redescription.

Euxoa recticincta; Lafontaine, 1980; = *E. teleboa*.

Description. Vestiture of head and thorax, and ground color of forewing reddish orange or cream-colored. Transverse lines, except median line, obscure or absent. Median line black, prominent. Terminal area and distal portion of subterminal area dusted with black scales. Reniform spot dark-filled, forming part of dark median line in most specimens. Hind wing of male white; hind wing of female white or dusted with gray-brown scales.

Expanse: 31.6±1.5 mm. Length of forewing: 15.7±0.8 mm (100 specimens).

Male genitalia (Fig. 80). Sacculus extension short, about as long as harpe in most specimens. Vesica with small nipple-like sub-basal diverticulum in addition to normal sub-basal diverticulum.

Length of right sacculus extension: 1.17±0.11 mm (20 specimens).

Length of left sacculus extension: 1.07±0.13 mm (20 specimens).

Length of right harpe: 1.25±0.06 mm (20 specimens).

Length of right sacculus: 1.29±0.07 mm (20 specimens).

Female genitalia (Figs. 111, 142). Sclerotized plate in ventral wall of ductus bursae extended as far anteriorly as plate in dorsal wall. Sclerotized flange-like projection on ovipositor valve rectangular, fin-like plate on posterior half of dorsal margin of valve. Flange-like projection pointed at posterior end, convex on dorsal margin and tapered abruptly to valve at anterior end.

Type material. The holotype of Carneades teleboa Smith is a female in the collection of the United States National Museum. The specimen has been dissected.

The holotype of Carneades pedalis Smith is a male in the collection of the United States National Museum. The specimen is without an abdomen.

The holotype of Carneades recticincta Smith is a female in the collection of the United States National Museum. The specimen has been dissected.

Distribution and period of flight. Euxoa teleboa occurs in the western Great Plains and eastern intermontane region from southern Saskatchewan and Alberta southward to northern Texas, central New Mexico, northern Arizona and east-central Nevada. A worn specimen in the Canadian National Collection is labelled "Peachland, B.C., 26 July, 1912, J.B. Wallis". Locality and collecting date both suggest that this specimen is mislabelled. Approximately 200 specimens from 42 localities were examined.

Adults have been collected from mid-August until late September.

Habitat. In the intermontane region, and in the Rocky Mountain region, Euxoa teleboa occurs in dry piñon-juniper woodland. In the Great Plains it inhabits arid areas in which the flora is dominated by sages (Artemisia spp.).

Remarks. Specimens of E. teleboa are most similar to those of E. tronella in color and markings, however, they may be distinguished readily by the broad, dark median line present in specimens of E. teleboa. Structurally, males of E. teleboa may be distinguished from those of E. tronella by the shorter sacculus extension and by the additional sub-basal diverticulum of the vesica. Shape of female ovipositor valve and shape of sclerotized, flange-like projection on valve may be used to distinguish females of the two species.

3.4.17. Euxoa moerens (Grote)

Figs. 41, 42, 43, 81, 112, 143, 172, 193

Carneades moerens Grote, 1883, p. 4; Arizona.

Carneades moerens; Smith, 1890b, p. 156; redescription.

Carneades moerens; Smith, 1893, p. 95; catalogue.

Paragrotis moerens; Dyar, 1902, p. 142.

Euxoa moerens; Hampson, 1903, p. 224.

Euxoa moerens; Draudt, 1924, p. 39; redescription.

Agrotis luteola Smith, 1887, p. 457; Arizona.

Carneades luteola; Smith, 1890b, p. 160; redescription.

Carneades luteola; Smith, 1893, p. 94; catalogue.

Paragrotis luteola; Dyar, 1902, p. 143.

Euxoa luteola; Hampson, 1903, p. 229.

Euxoa luteola; Barnes and McDunnough, 1917, p. 41; = E. moerens.

Description. Antenna of male slightly biserrate. Vestiture of head and thorax brownish gray. Ground color of forewing pale gray, pale brown, or orange-brown, dusted with darker scales. Transverse lines indistinct. Terminal area gray-brown, slightly darker than ground color of forewing. Reniform and orbicular spots concolorous with ground color in most specimens, outlined in black. Hind wing buff with dusting of pale smoky-brown scales on outer third of wing and in many specimens on median line as well. Hind wing smoky-brown, slightly paler near base, in some specimens.

Expanse: 29.8±1.2 mm. Length of forewing: 14.6±0.7 mm

(100 specimens).

Male genitalia (Fig. 81). Uncus with stout setae mesially, brush-like in appearance. Harpe curved dorsally near apex; harpe with about 30 scattered setae. Cucullus strap-like, not markedly constricted subapically. Vesica with small nipple-like sub-basal diverticulum in addition to normal foot-like sub-basal diverticulum.

Length of right sacculus extension: 1.53±0.07 mm (20 specimens).

Length of left sacculus extension: 1.52±0.07 mm (20 specimens).

Length of right harpe: 1.06±0.04 mm (20 specimens).

Length of right sacculus: 1.23±0.06 mm (20 specimens).

Female genitalia (Figs. 112, 143). Corpus bursae oval; ductus bursae entering corpus bursae about one-quarter from posterior end. Sclerotized plate in dorsal wall of ductus bursae extended farther anteriorly than plate in ventral wall. Sclerotized flange-like projection on ovipositor valve elongate, fin-like, tapered abruptly to valve at anterior end in many specimens.

Type material. The holotype of Carneades moerens Grote is a male in the collection of the United States National Museum. The specimen has been dissected.

The holotype of Agrotis luteola Smith is a female in the collection of the United States National Museum. The specimen has been dissected.

Distribution and period of flight. Euxoa moerens occurs in the western Great Plains from southern Saskatchewan and Alberta southward to central Colorado, and in the intermontane region from southern Idaho and central Oregon southward to central Colorado, northern

Arizona and central Nevada. Approximately 250 specimens from 37 localities were examined.

Specimens have been collected from mid-August until late September.

Habitat. *Euxoa moerens* inhabits open pinon-juniper woodland where sagebrush is abundant. It also occurs in mixed conifer forests of pinon pine (*Pinus* spp.), Utah juniper (*Juniperus osteosperma* (Torr.) Little) and ponderosa pine (*Pinus ponderosa* Dougl.). In the Great Plains region it occurs in open aridlands where sage (*Artemisia* spp.) is abundant.

Remarks. Specimens of *Euxoa moerens* are most similar to those of *E. latro* in wing markings and structural characters. Specimens of the two species may be distinguished by characters in key.

3.4.18. Euxoa latro (Barnes and Benjamin)

Figs. 44, 45, 82, 113, 144, 173, 193

Agrotis latro Barnes and Benjamin, 1926, p. 305; Truckee, California.
Euxoa latro; McDunnough, 1938, p. 58.

Description. Antenna of male slightly biserrate. Vestiture of head and thorax mixture of gray, brown and black scales. Ground color of forewing brown or gray-brown markedly dusted with black. Transverse lines present; median line conspicuous in most specimens. Orbicular spot concolorous with ground color. Reniform spot pale, cream-colored or pale buff in many specimens. Hind wing smoky-brown.

Expanse: 30.9±1.3 mm. Length of forewing: 15.3±0.8 mm (80 specimens).

Male genitalia (Fig. 82). Uncus with stout setae mesially, brush-like in appearance. Harpe evenly incurved throughout its length, not curved dorsally near apex. Harpe bristly in appearance, its surface covered with 50-60 setae. Cucullus bat-like, markedly constricted subapically. Vesica only with normal, foot-like sub-basal diverticulum in most specimens, trace of extra nipple-like diverticulum in some specimens.

Length of right sacculus extension: 1.55±0.09 mm (20 specimens).
Length of left sacculus extension: 1.52±0.09 mm (20 specimens).
Length of right harpe: 0.96±0.05 mm (20 specimens).
Length of right sacculus: 1.34±0.06 mm (20 specimens).

Female genitalia (Figs. 113, 144). Indistinguishable from those of *E. moerens* female.

Type material. The holotype of *Agrotis latro* Barnes and Benjamin is a male in the collection of the United States National Museum. The specimen has been dissected.

Distribution and period of flight. *Euxoa latro* occurs in the Cascades and Sierra Nevada Mountain systems from central Washington southward to southern California. A disjunct population occurs in the La Sal Mountains, Utah (Fig. 173). Approximately 200 specimens from 18 localities were examined.

Most specimens were collected between mid-August and mid-September. One specimen was collected in mid-October.

Habitat. *Euxoa latro* inhabits conifer forests of pine and fir.

Remarks. Specimens of *Euxoa latro* may be distinguished from those of *E. moerens* by characters in key. In general, the much darker coloration of *Euxoa latro* specimens allow them to be readily distinguished from *E. moerens* specimens. Although the two species rarely occur together, they have been collected together in the Sierra Nevadas where the ponderosa pine zone meets the piñon-juniper zone.

3.4.19. Euxoa murdocki (Smith)

Figs. 46, 83, 114, 145, 174

Agrotis murdocki Smith, 1890a, p. 49; British Columbia, Utah.

Carneades murdocki; Smith, 1890b, p. 174; redescription.

Carneades murdocki; Smith, 1893, p. 99; catalogue.

Paragrotis murdocki; Dyar, 1902, p. 145.

Euxoa murdocki; Hampson, 1903, p. 247.

Euxoa murdocki; Draudt, 1924, p. 45; redescription.

Description. Antenna of male slightly biserrate. Vestiture of head and thorax orange-brown or yellow-brown. Ground color of forewing orange in basal and subterminal areas, gray in median and terminal areas. Transverse lines prominent; median line dark gray. Reniform and orbicular spots partially outlined in black, inconspicuous. Reniform spot dark gray, concolorous with median line. Orbicular spot pale gray, concolorous with median area. Hind wing smoky-brown, paler near base in most specimens.

Expanse: 29.0±1.5 mm. Length of forewing: 14.1±0.7 mm (100 specimens).

Male genitalia (Fig. 83). Similar to those of E. moerens male but sacculus larger and vesica with normal, foot-like sub-basal diverticulum only.

Length of right sacculus extension: 1.48±0.10 mm (20 specimens).

Length of left sacculus extension: 1.48±0.09 mm (20 specimens).

Length of right harpe: 1.05±0.05 mm (20 specimens).

Length of right sacculus: 1.38±0.05 mm (20 specimens).

Female genitalia (Figs. 114, 145). Indistinguishable from those of *E. moerens* and *E. latro* females.

Type material. *Agrotis murdocki* Smith was described from a male from British Columbia and a female from Utah. Both specimens are in the collection of the United States National Museum. A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa murdocki* occurs from south-central British Columbia southward to west-central Colorado, central Nevada and southern California (Fig. 174). I have seen only one specimen collected east of the Continental Divide, this from Banff, Alberta. Approximately 250 specimens from 41 localities were examined.

Specimens have been collected from late August until mid-October.

Habitat. *Euxoa murdocki* is found most commonly in conifer forests of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and ponderosa pine (*Pinus ponderosa* Dougl.). In the Great Basin it occurs in piñon-juniper woodland.

Remarks. Although *Euxoa murdocki* specimens are structurally similar to those of *E. moerens* and *E. latro*, they are unlike those of any other species in the genus in wing color. The combination of orange basal and subterminal areas and gray median and terminal areas make this species one of the easiest to recognize in *Euxoa*.

3.4.20. *Euxoa dodi* McDunnough

Figs. 47, 84, 115, 146, 175, 194

Euxoa dodi McDunnough, 1923, p. 163; Lethbridge, Alberta.

Euxoa dodi; Draudt, 1924, p. 43; redescription.

Description. Antenna of male biserrate. Vestiture of head and thorax buff or brown. Ground color of forewing brown or pale gray-brown. Transverse lines all prominent except median line. Basal and subterminal areas slightly paler than median area. Terminal area dark gray-brown. Reniform, orbicular and claviform spots outlined in black, concolorous with basal and subterminal areas. Hind wing pale smoky-brown, slightly darker on outer quarter of wing.

Expanse: 30.3±1.2 mm. Length of forewing: 14.9±0.7 mm (80 specimens).

Male genitalia (Fig. 84). Uncus with long, thin setae mesially. Harpe pubescent, in addition to longer scattered setae. Right sacculus extension less than 1 1/2 times length of right harpe. Vesica without extra nipple-like sub-basal diverticulum.

Length of right sacculus extension: 1.59±0.10 mm (20 specimens).

Length of left sacculus extension: 1.45±0.12 mm (20 specimens).

Length of right harpe: 1.17±0.05 mm (20 specimens).

Length of right sacculus: 1.31±0.06 mm (20 specimens).

Female genitalia (Figs. 115, 146). Ductus bursae and corpus bursae similar to those of *E. moerens*, *E. latro* and *E. murdocki* females. Ovipositor valve clothed with fine setae, without sclerotized projection at apex.

Type material. The holotype of Euxoa dodi McDunnough is a male (type No. 608) in the Canadian National Collection, Ottawa. The specimen has been dissected.

Distribution and period of flight. Euxoa dodi occurs from southern Saskatchewan and Alberta southward to southern North Dakota, southern New Mexico and northern Arizona (Fig. 175). Approximately 110 specimens from 36 localities were examined.

Specimens have been collected from mid-August until early September.

Habitat. Euxoa dodi occurs in areas of dry, shortgrass prairie where sage (Artemisia spp.) is abundant. It also occurs in the Rocky Mountain foothills where prairie habitat occurs in open pine parkland.

Remarks. Specimens of E. dodi may be distinguished from those of E. infracta by paler coloration and lack of copper suffusion of the forewing and by the male genitalia. The sacculus extension of E. dodi male is less than 1 1/2 times length of harpe; it is more than 1 1/2 times length of harpe in E. infracta male. In general, Euxoa dodi occurs in more open xeric habitats than does E. infracta. Specimens of E. dodi from central Colorado are darker than are those from the Great Plains. At present it is not known whether E. dodi and E. infracta hybridize in this region or if these specimens represent a dark form of E. dodi.

3.4.21. *Euxoa infracta* (Morrison)

Figs. 48, 85, 116, 147, 176, 194

Agrotis infracta Morrison, 1875a, p. 115; Colorado, Texas.

Carneades infracta; Smith, 1890b, p. 160; redescription.

Carneades infracta; Smith, 1893, p. 94; catalogue.

Paragrotis infracta; Dyar, 1902, p. 142.

Euxoa infracta; Hampson, 1903, p. 228.

Euxoa infracta; Draudt, 1924, p. 40; redescription.

Description. Antenna of male biserrate. Vestiture of head and thorax dark blackish brown. Ground color of forewing brown; basal and subterminal areas brown with a copper suffusion, median and terminal areas dark blackish brown. Transverse lines all prominent except median line. Reniform, orbicular and claviform spots outlined in black, slightly paler than median area. Hind wing smoky-brown, slightly paler near base in many specimens.

Expanse: 31.4±1.3 mm. Length of forewing: 15.7±0.8 mm (100 specimens).

Male genitalia (Fig. 85). Similar to those of *E. dodi* male but sacculus extension longer and harpe shorter in *E. infracta* male. Right sacculus extension longer than 1 1/2 times length of right harpe.

Length of right sacculus extension: 1.62±0.10 mm (20 specimens).

Length of left sacculus extension: 1.60±0.10 mm (20 specimens).

Length of right harpe: 0.99±0.06 mm (20 specimens).

Length of right sacculus: 1.36±0.07 mm (20 specimens).

Female genitalia (Figs. 116, 147). Indistinguishable from those of *E. dodi* female.

Type material. *Agrotis infracta* Morrison was described from two specimens, one from Colorado and one from Texas. Only the specimen from Colorado has been located. This specimen, a female in good condition except for missing antenna, is labelled "Col.", "type", "*Carneades infracta* Morr. 1782", "*Euxoa* slide MSU 3". This specimen, in the collection of Michigan State University, East Lansing, is here designated lectotype.

Distribution and period of flight. *Euxoa infracta* occurs from southern Manitoba westward to British Columbia and southward to northern New Mexico, east-central Arizona, central Nevada and east-central California (Fig. 176). Approximately 450 specimens from 97 localities were examined.

Specimens have been collected from mid-July until late September.

Habitat. *Euxoa infracta* is found most commonly in conifer forests of pine and fir. In the intermontane region it also occurs in pine and aspen forests.

Remarks. Specimens of *Euxoa infracta* may be distinguished from those of *E. dodi* by characters in key (see also remarks under *E. dodi*).

3.4.22. Euxoa laetificans (Smith)

Figs. 49, 50, 86, 117, 150, 177, 195

Carneades laetificans Smith, 1894, p. 48; Glenwood Springs, Colorado.

Paragrotis laetificans; Dyar, 1902, p. 140.

Euxoa laetificans; Hampson, 1903, p. 208.

Euxoa laetificans; Draudt, 1924, p. 38; redescription.

Carneades masculinus Smith, 1903b, p. 6; Silver Bow Co., Montana; Yakima, Washington, southern Utah.

Euxoa masculinus; Barnes and McDunnough, 1917, p. 41; = E. laetificans.

Carneades masculinus; Rindge, 1955, p. 120; type material.

Description. Sexually dimorphic. Vestiture of head gray; vestiture of prothoracic collar reddish brown (male) or gray (female); vestiture of thorax gray or reddish gray. Ground color of forewing light reddish brown (male) or gray (female). Transverse lines absent in most specimens, trace of lines in some specimens. Median area around reniform and orbicular spots shaded with black. Terminal area dark gray, streaked into subterminal area. Costa and cubital vein paler than remainder of forewing, yellow-brown (male) or silver-gray (female). Cubital vein pale from wing base to reniform spot. Reniform and orbicular spots with pale line between black outline and gray center; orbicular spot fused with costal shade in some specimens. Basal dash and claviform spot black, prominent. Hind wing of male white or pale buff with some smoky-brown shading on terminal margin. Hind wing of female smoky-brown to base.

Expanse: 30.6±1.5 mm. Length of forewing: 14.5±0.7 mm (100 specimens).

Male genitalia (Fig. 86). Sacculus extensions and harpes long; harpe pubescent. Vesica without nipple-like sub-basal diverticulum, only foot-like diverticulum sub-basally. Median diverticulum with basal bulge in many specimens.

Length of right sacculus extension: 1.71±0.10 mm (20 specimens).

Length of left sacculus extension: 1.65±0.12 mm (20 specimens).

Length of right harpe: 1.45±0.05 mm (20 specimens).

Length of right sacculus: 1.45±0.05 mm (20 specimens).

Female genitalia (Figs. 117, 150). Corpus bursae oval or rectangular, enlarged posterolaterally on left side. Ovipositor valve clothed with short, fine setae, without sclerotized projection at apex. Valve triangular, pointed toward apex.

Type material. *Carneades laetificans* was described by Smith from two specimens, a male and a female from Colorado. Both specimens are in the collection of the United States National Museum. A lectotype will be selected by Todd (1980).

Carneades masculinus Smith was described from seven males from Montana, Washington and Utah. Type material is in the collections of the American Museum of Natural History and the United States National Museum. A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa laetificans* occurs in western North America from southern Saskatchewan westward to southern British Columbia and southward to southern Colorado, Utah, Nevada, and east-central California (Fig. 177). Approximately 700 specimens from 71 localities were examined.

Specimens have been collected from late July until mid-September.

Habitat. Euxoa laetificans is found most commonly in open pine forests of ponderosa and lodgepole pine (Pinus ponderosa Dougl. and P. contorta Dougl.). It is collected in areas of coarse, gravelly soil. In the intermontane region E. laetificans occurs in piñon-juniper woodland as well as in pine forests.

Remarks. Specimens of Euxoa laetificans are similar to those of E. quadridentata but may be distinguished from them by lack of pale-lined veins in subterminal area and by characters of genitalia. The harpe of E. laetificans male is pubescent and harpe and sacculus extensions are much longer than are those of E. quadridentata male. Ovipositor valve of E. laetificans female is narrow and pointed apically; that of E. quadridentata female is broad and rounded apically.

Larvae have been reared on alfalfa (Medicago sativa L.), sweet clover (Melilotus spp.), beet (Beta vulgaris L.), lettuce (Lactuca sativa L.) and Russian thistle (Salsola kali L.) (Cook, 1930b).

3.4.23. *Euxoa quadridentata* (Grote and Robinson)

Figs. 51, 52, 87, 118, 148, 149, 178, 195

Agrotis quadridentata Grote and Robinson, 1865, p. 491; Colorado.

Carneades quadridentata; Smith, 1890b, p. 139; redescription.

Carneades quadridentata; Smith, 1893, p. 89; catalogue.

Paragrotis quadridentata; Dyar, 1902, p. 140.

Euxoa quadridentata; Hampson, 1903, p. 209.

Euxoa quadridentata; Draudt, 1924, p. 38; redescription.

Carneades pugionis Smith, 1900, p. 419; Denver, Colorado; Calgary, Alberta.

Paragrotis pugionis; Dyar, 1902, p. 141.

Euxoa pugionis; Hampson, 1903, p. 209.

Euxoa pugionis; Barnes and McDunnough, 1917, p. 41; = *E. quadridentata*.

Carneades pugionis; Rindge, 1955, p. 127; type material.

Euxoa flutea Smith, 1910b, p. 255; Sierra Nevada, California.

Euxoa quadridentata flutea; Barnes and McDunnough, 1917, p. 41.

Euxoa quadridentata flutea; Draudt, 1924, p. 38; redescription.

Euxoa flutea; Rindge, 1955, p. 127; type material.

Description. Sexually dimorphic. Vestiture of head gray; upper half of prothoracic collar gray-brown, basal half yellow (male) or pale gray (female). Vestiture of thorax mixture of brown, black and gray scales. Ground color of forewing dark brown streaked with yellow (male) or silver-gray (female). Transverse lines indistinct. Veins Cu_1 and M_3 pale-lined with silver-gray in both sexes and projected into terminal area; cubital vein silver-gray. In male, costal area, posterior margin of wing, and area distal to claviform spot pale yellow or yellow-buff; subterminal area streaked with yellow or pale buff. In female, pale yellow shading replaced by silver-gray. Terminal area dark gray-brown, streaked into subterminal area; apices of streaks in subterminal area black. Reniform and orbicular spots filled with yellow-buff, or with yellow-buff between gray center and black outline. Black basal dash present, inconspicuous in some specimens. Claviform spot black. Hind wing in most males white basally with smoky-brown shading on outer third of wing. Hind wing of female and of male from Sierra Nevada populations dark smoky-brown.

Expanse: 30.7±1.1 mm. Length of forewing: 15.2±0.6 mm (100 specimens).

Male genitalia (Fig. 87). Harpe and sacculus extension much shorter than those of E. laetificans male; harpe not pubescent. Vesica without extra nipple-like sub-basal diverticulum.

Length of right sacculus extension: 1.22±0.13 mm (24 specimens).

Length of left sacculus extension: 1.18±0.13 mm (24 specimens).

Length of right harpe: 1.18±0.05 mm (24 specimens).

Length of right sacculus: 1.35±0.07 mm (24 specimens).

Female genitalia (Figs. 118, 148, 149). Corpus bursae somewhat rectangular. Sclerotized plates in dorsal and ventral wall of ductus bursae short, not extended farther anteriorly than anterior apophyses. Ovipositor valve clothed with fine setae, a short, sclerotized flange-like projection at valve apex in females from populations of nominate subspecies (see below).

Type material. *Agrotis quadridentata* Grote and Robinson was described from an undetermined number of males and one female. Of the type material, only one male has been located, this in the collection of the Academy of Natural Sciences of Philadelphia. This specimen, labelled "Col.", "type No. 7596, *Agrotis quadridentata* ♂, A.R. Grote & Rob.", "genitalia slide *Euxoa* 5202 ♂", is here designated lectotype.

Carneades pugionis Smith was described from seven males. Type material is in the collections of the American Museum of Natural History and the United States National Museum. A lectotype will be designated by Todd (1980).

Euxoa flutea Smith was described from two females; these are in the collection of the American Museum of Natural History. A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa quadridentata* occurs in western North America from eastern North Dakota and southern Manitoba westward to British Columbia and southward to southern New Mexico, Arizona and California (Fig. 178). Approximately 1400 specimens from 138 localities were examined.

Specimens have been collected from mid-August until early October.

Habitat. *Euxoa quadridentata* occurs in the Great Plains and Great Basin in open prairie or sagebrush areas and in open piñon-juniper woodland. In the Cascades and Sierra Nevada Mountains it occurs in lodgepole pine (*Pinus contorta* Dougl.) forests.

Remarks. Specimens of *Euxoa quadridentata* may be distinguished from those of *E. laetificans* by characters in key (see also remarks under *E. laetificans*).

Larvae have been reared on wheat (*Triticum aestivum* L.) in Montana (Cook, 1930b).

Populations of *E. quadridentata* may be arranged in two subspecies. Differences in ovipositor valves of the two subspecies suggest that females may oviposit in different soil types. Hybridization experiments and longer series of females from eastern Nevada would help to clarify the status of the two subspecies. Relative scarcity of females of this species has hampered such studies. Of 1400 specimens examined, about 150 were females. Only four females were located from eastern Nevada. The subspecies of *E. quadridentata* are as follows:

Euxoa quadridentata quadridentata (Grote and Robinson)

Agrotis quadridentata Grote and Robinson, 1865, p. 491.
Carneades pugionis Smith, 1900, p. 419.

The nominate subspecies occurs in the Great Plains, the Rocky Mountain region and the eastern intermontane region as far west as eastern British Columbia, western Montana and Wyoming, eastern Nevada and northwestern Arizona (Fig. 195). Specimens from populations of this subspecies can be distinguished from those of the western subspecies only by form of female ovipositor valve. The ovipositor valve of *E. q. quadridentata* female has a short, sclerotized, flange-like projection at apex of valve (Fig. 148). That of *E. q. flutea* female lacks this sclerotized projection (Fig. 149).

Euxoa quadridentata flutea Smith

Euxoa flutea Smith, 1910b, p. 255.

This subspecies occurs in the Cascades and Sierra Nevada Mountains, and in the intermontane region as far east as south-central British Columbia, western Idaho and eastern Nevada (Fig. 195). Specimens of *E. q. flutea*, unlike those of *E. q. quadridentata*, have darker hind wings in more mesic habitats.

3.4.24. Euxoa inscripta Lafontaine, new species

Figs. 53, 54, 88, 119, 151, 179, 196

Description. Antenna of male biserrate and bifasciculate. Antenna of female filiform. Frontal tubercle present. Vestiture of head and thorax mixture of gray and brown scales.

Ground color of forewing brown dusted with black. Basal line, transverse anterior and transverse posterior lines, and subterminal line indistinct. Median line absent. Cubital vein pale, remainder of veins lined with black. Terminal area dark gray-brown, streaked into subterminal area; portion of streaks in subterminal area black in most specimens. Reniform and orbicular spots with pale brown shading between dark brown central spot and black outline. Orbicular spot oval in most specimens. Claviform spot black, prominent in most specimens.

Hind wing of male white basally with sharply defined smoky-brown band on terminal third or quarter of wing. Hind wing of female smoky-brown.

Expanse: 30.6±1.4 mm. Length of forewing: 15.2±0.6 mm (80 specimens).

Male genitalia (Fig. 88). Right and left sacculus extensions similar in length, longer than harpes. Vesica without extra nipple-like sub-basal diverticulum; median diverticulum with basal bulge.

Length of right sacculus extension: 1.52±0.09 mm (20 specimens).

Length of left sacculus extension: 1.53±0.10 mm (20 specimens).

Length of right harpe: 1.18±0.04 mm (20 specimens).

Length of right sacculus: 1.46±0.08 mm (20 specimens).

Female genitalia (Figs. 119, 151). Corpus bursae somewhat rectangular; junction of ductus bursae and corpus bursae about 1/4 from posterior end of corpus bursae. Ovipositor valve with fine setae, sclerotized flange-like projection at apex.

Type material. Holotype male, Craig, Colo., 22 mi N., 7100 ft, 15 Aug. 1965 (D.F. Hardwick), type No. 15940 in the Canadian National Collection, Ottawa. Paratypes: 70 males, 33 females: COLORADO: Craig, 22 mi N., 7100 ft, 15 Aug. 1965 (D.F. Hardwick); Dinosaur, 4 mi NE., 7000 ft, 18 Aug. 1965 (D.F. Hardwick); Maybell, 6 mi SE., 6200 ft, 17 Aug. 1965 (D.F. Hardwick); Sapinero, 5 mi ENE., 7700 ft, 15 Aug. 1971 (D.F. Hardwick); Sargents, 3 mi NE., 9700 ft, 14 Aug. 1971 (D.F. Hardwick). MONTANA: NE side Howie Rd., 1/4 mi from Gibson Rd., 4500 ft, Sweet Grass Co., 21 Aug. 1969 (J.G. Franclemont). UTAH: Salina, 13 mi SE., 7400 ft, 26 Aug. 1965 (D.F. Hardwick). WYOMING: Alcova, 4 mi SW., 5500 ft, 14 Aug. 1965 (D.F. Hardwick); Kemmerer, 8 mi SW., 6800 ft, 23 Aug. 1964 (D.F. & V.J. Hardwick); Lander, 10 mi SE., 5600 ft, 31 Aug. 1964 (D.F. & V.J. Hardwick); Sage, 6 mi N., 6200 ft, 22 Aug. 1964 (D.F. Hardwick).

The holotype and most of the paratypes are in the Canadian National Collection. One paratype is in the collection of J.G. Franclemont, Ithaca, New York.

Distribution and period of flight. *Euxoa inscripta* occurs from southern Montana southward to western Colorado and central Utah; it also occurs in west-central Nevada and east-central California (Fig. 179). One hundred and fourteen specimens from 15 localities were examined.

Specimens have been collected from mid-August until late August.

Habitat. Euxoa inscripta occurs in arid areas where sagebrush (Artemisia spp.) is abundant. It is found in areas of coarse, gravelly soil.

Remarks. In wing pattern, specimens of E. inscripta are similar to those of E. olivalis but may be distinguished from them by rounded orbicular spot and by lack of silver-gray streaking. In structural characters, males of E. inscripta are most similar to those of E. unica but may be distinguished by longer, symmetrical sacculus extensions.

The specific name inscripta refers to the fine, black lines on wing veins and maculation.

Specimens from California and Nevada have darker, more gray forewings than do those from more easterly populations and pale shading between central dark spot and black outline of reniform and orbicular spots is white in many specimens rather than pale brown.

3.4.25. Euxoa unica McDunnough

Figs: 57, 89, 179, 196

Euxoa unica McDunnough, 1940, p. 192; Saskatoon, Saskatchewan.

Description. Male antenna markedly biserrate. Vestiture of head, upper half of prothoracic collar and thorax brown; basal half of prothoracic collar yellowish brown. Ground color of forewing light brown dusted with darker brown, especially around reniform and orbicular spots. Transverse lines present. Terminal area dark brown, blackish brown sagittate spots on proximal side of subterminal line. Costa and cubital vein yellowish buff. Reniform and orbicular spots pale buff. Claviform spot black. Basal dash small, black. Hind wing white with smoky-brown shading on terminal quarter of wing and on veins.

Expanse: 31, 33 mm. Length of forewing: 15, 16 mm (2 specimens).

Male genitalia (Fig. 89). Similar to those of E. inscripta male but sacculus extensions shorter and asymmetrical, left sacculus extension much shorter than right.

Length of right sacculus extension: 1.52, 1.38 mm (2 specimens).

Length of left sacculus extension: 1.28, 1.08 mm (2 specimens).

Length of right harpe: 1.38, 1.25 mm (2 specimens).

Length of right sacculus: 1.58, 1.48 mm (2 specimens).

Female genitalia. Female genitalia of E. unica unknown but would probably be similar to those of E. inscripta female.

Type material. The holotype of *Euxoa unica* McDunnough is a male (type No. 5071) in the Canadian National Collection, Ottawa.

Distribution and period of flight. *Euxoa unica* is known from two males, both collected in the vicinity of Saskatoon, Saskatchewan. Specimens were collected 23 Aug. 1937 (holotype) and 26 Aug. 1942.

Remarks. The rarity of *Euxoa unica* is puzzling. The northern Great Plains region, including central Saskatchewan, has been well collected in August and September; a light trap was run for many years at Saskatoon and only two specimens of *E. unica* were collected. While there are species known from comparably restricted, formerly glaciated, areas (e.g. southern Manitoba, see section 5.6.4.), other explanations for its apparent rarity must be considered.

Specimens of *E. unica* differ from those of other species in the *E. detersa* group in that male antenna is more prominently biserrate and male sacculus extensions are markedly asymmetrical. In these features, *E. unica* males resemble those of *E. intrita* (Morrison). Specimens of *E. intrita*, however, differ from those of *E. unica* and other species in the *E. detersa* group in many ways: antenna more prominently biserrate; forewing shorter and broader; male sacculus extensions much stouter and more markedly asymmetrical than are those of *E. unica*; harpes longer; sacculus stouter; sub-basal diverticulum of vesica T-shaped with projections directed both dorsally and ventrally.

Specimens of *E. intrita* are variable in wing markings; of about 600 specimens in the Canadian National Collection, only about 10 have wing markings that resemble those of *E. unica* specimens; these are from Saskatoon.

If *E. unica* specimens are of hybrid origin, *Euxoa niveilinea* (Grote) and *E. dargo* (Strecker) appear to be the two most likely candidates for being the other parent in an *E. intrita* group-*E. detersa* group cross.

The *E. intrita* group is well-removed from the *E. detersa* group in the reconstructed phylogeny of *Euxoa* (see figure 199) and successful intergroup hybridization in *Euxoa* is at present unknown. While hybrid origin for *E. unica* specimens cannot be demonstrated, further work in this area would be worthwhile.

3.4.26. *Euxoa niveilinea* (Grote)

Figs. 55, 56, 90, 120, 152, 180

Agrotis niveilinea Grote, 1882, p. 216; Arizona.

Carneades niveilinea; Smith, 1890b, p. 139; redescription.

Carneades niveilinea; Smith, 1893, p. 89; catalogue.

Paragrotis niveilinea; Dyar, 1902, p. 140.

Euxoa niveilinea; Hampson, 1903, p. 210.

Euxoa niveilinea; Draudt, 1924, p. 37; redescription.

Euxoa rabiata Smith, 1910b, p. 255; Volga, South Dakota; Colorado; Calgary, Alberta.

Euxoa niveilinea rabiata; Barnes and McDunnough, 1917, p. 41.

Euxoa niveilinea rabiata; Draudt, 1924, p. 38; redescription.

Euxoa niveilinea rabiata; McDunnough, 1950, p. 374; redescription.

Agrotis rabiata; Forbes, 1954, p. 38; good species.

Euxoa rabiata; Rindge, 1955, p. 128; type material.

Euxoa rabiata; Lafontaine, 1980; = *E. niveilinea*.

Description. Vestiture of head and thorax brownish gray; transverse band of white scales on thorax posterior to prothoracic collar. Ground color of forewing dark brownish gray dusted with black. Transverse lines obscure in most specimens. Basal and median areas concolorous; subterminal area slightly paler than median area; terminal area dark gray, series of black, sagittate spots in subterminal area on proximal side of subterminal line in many specimens. Costa extensively dusted with silver-gray in many specimens. Veins

Cu, Cu_1 and M_3 pale-lined, latter two projected into terminal area. Reniform and orbicular spots concolorous with subterminal area. Claviform spot black, obscure. Basal dash obscure or absent. Hind wing of both sexes white with smoky-brown shading on terminal line and veins in most specimens.

Expanse: 30.8±1.2 mm. Length of forewing: 15.6±0.6 mm (100 specimens).

Male genitalia (Fig. 90). Harpe markedly bent mesially, basal half of right harpe forming an angle of about 90° with right sacculus extension in most males. Right sacculus extension long, curved toward valve apically. Vesica with extra, nipple-like sub-basal diverticulum and with basal bulge on median diverticulum.

Length of right sacculus extension: 1.78±0.10 mm (20 specimens).

Length of left sacculus extension: 1.75±0.10 mm (20 specimens).

Length of right harpe: 1.11±0.07 mm (20 specimens).

Length of right sacculus: 1.39±0.07 mm (20 specimens).

Female genitalia (Figs. 120, 152). Corpus bursae slightly constricted mesially. Ovipositor valve clothed with fine setae, sclerotized flange-like projection at apex.

Type material. Agrotis niveilinea Grote was described from "nearly a dozen" specimens. Of these, four males have been located in the collection of the United States National Museum. A male labelled "Arizona", "Col. B. Neumoegen", "type No. 33736 U.S.N.M.", "Agrotis niveilinea Grote ♂ type", "♂ genitalia on slide Apr. 1966 ELT 2172" is here designated lectotype.

Euxoa rabiata Smith was described from six males and two females.

Four male syntypes are in the collection of the American Museum of Natural History. A lectotype will be selected by Todd (1980).

Distribution and period of flight. *Euxoa niveilinea* occurs in the Great Plains region from southern Saskatchewan and Alberta southward to northern Texas and southern New Mexico. Its range extends eastward from the Great Plains region into the "prairie peninsula" of central Michigan and westward in the intermontane region to central Arizona. An apparently disjunct population occurs in relict prairie habitat in southeastern Texas (Fig. 180). Approximately 700 specimens from 66 localities were examined.

Specimens have been collected from late August until late October.

Habitat. *Euxoa niveilinea* inhabits dry, sandy prairie areas where sage (*Artemisia* spp.) is abundant.

Remarks. Specimens of *Euxoa niveilinea* are most easily confused with those of *E. dargo* and *E. cicatricosa*. Males of *E. niveilinea* may be distinguished from those of *E. dargo* and *E. cicatricosa* by long sacculus extension; females may be distinguished by flange-like projection rather than stout setae on ovipositor valve. Most specimens of *E. niveilinea* can be distinguished from those of *E. dargo* by pale rather than dark hind wing and from those of *E. cicatricosa* by presence of transverse band of white scales on the thorax posterior to the prothoracic collar lacking in *E. cicatricosa* specimens.

3.4.27. Euxoa dargo (Strecker)

Figs. 58, 91, 121, 153, 181, 197

Agrotis dargo Strecker, 1898, p. 6; Loveland, Colorado.

Paragrotis dargo; Dyar, 1902, p. 140.

Euxoa dargo; Barnes and McDunnough, 1917, p. 41.

Euxoa dargo; Draudt, 1924, p. 37; redescription.

Agrotis dargo; Forbes, 1954, p. 38; redescription.

Carneades rumatana Smith, 1903c, p. 203; Volga, South Dakota; Calgary, Alberta.

Euxoa rumatana; Barnes and McDunnough, 1917, p. 41; = E. dargo.

Carneades rumatana; Rindge, 1955, p. 129; type material.

Description. Head, thorax and pattern of forewing similar to that of E. niveilinea but ground color dark brown. Claviform spot with pale buff streak distal to it. Hind wing of most males buff basally with sharply delimited smoky-brown band on terminal third or half of wing. Hind wing of some males smoky-brown almost to base. Hind wing of female smoky-brown, slightly paler at base.

Expanse: 27.2±1.5 mm. Length of forewing: 13.7±0.8 mm (100 specimens).

Male genitalia (Fig. 91). Harpe and sacculus extension short. Vesica with extra nipple-like sub-basal diverticulum and with basal bulge on median diverticulum.

Length of right sacculus extension: 1.16±0.10 mm (20 specimens).

Length of left sacculus extension: 1.09±0.10 mm (20 specimens).

Length of right harpe: 0.93±0.08 mm (20 specimens).

Length of right sacculus: 1.10±0.06 mm (20 specimens).

Female genitalia (Figs. 121, 153). Corpus bursae oval, slightly invaginated on left side in most specimens. Ovipositor valve with stout setae apically; sub-basal row of long setae stout and spike-like.

Type material. *Agrotis dargo* was described by Strecker from "a number of examples". Of this material, two males and two females are in the collection of the Field Museum of Natural History, Chicago. A male labelled "Col.", "*A. dargo* type Streck.", is here designated lectotype. The specimen is in good condition; it has been dissected.

Carneades rumatana Smith, was described from sixteen males and one female. Type material is in the collections of the American Museum of Natural History, the United States National Museum and the Canadian National Collection. A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa dargo* occurs in western North America from southern Manitoba westward to southern British Columbia and southward to central Nebraska, northern New Mexico, southern Idaho and east-central Oregon (Fig. 181). Approximately 350 specimens from 60 localities were examined.

Specimens have been collected from late August until early October.

Habitat. *Euxoa dargo* inhabits dry prairie or sagebrush (*Artemisia* spp.) areas. In the southern portion of its range it is found in areas where prairie habitat occurs in open pine parkland.

Remarks. Specimens of *E. dargo* resemble those of *E. niveilinea* and *E. cicatricosa* but may be distinguished from them by characters in key (see also remarks under *E. niveilinea*). Most specimens of *E. dargo* can be distinguished from those of *E. niveilinea* by darker hind wing and by pale streak distal to claviform spot.

3.4.28. Euxoa melura McDunnough

Figs. 59, 92, 122, 154, 182, 197

Euxoa melura McDunnough, 1932, p. 231; Eureka, Utah.

Description. Head, thorax and wing markings almost identical to those of E. olivalis (page 73) specimens except claviform spot larger, filled with dark gray, and orbicular spot round or slightly oval in most specimens rather than elongate and bar-like. Specimen illustrated is one of few with elongate orbicular spot (see Fig. 59).

Expanse: 31.2±1.4 mm (20 specimens). Length of forewing: 15.5±0.5 mm (32 specimens).

Male genitalia (Fig. 92). Unlike those of any other species in E. detersa group. Harpe elongate, almost straight. Sacculus extension short, about 2/3 length of harpe. Vesica with extra sub-basal diverticulum; without basal pouch on median diverticulum.

Length of right sacculus extension: 0.93±0.08 mm (11 specimens).

Length of left sacculus extension: 0.83±0.10 mm (10 specimens).

Length of right harpe: 1.37±0.05 mm (11 specimens).

Length of right sacculus: 0.99±0.05 mm (11 specimens).

Female genitalia (Figs. 122, 154). Similar to those of E. dargo but corpus bursae not invaginated on left side; ovipositor valve with sub-basal row of long setae mostly thin and hair-like, only 3 or 4 setae at anteroventral corner of valve stout.

Type material. The holotype of Euxoa melura McDunnough is a male in the Canadian National Collection, Ottawa (type No. 3363).

Distribution and period of flight. The distribution of *E. melura* is poorly known. It has been collected in southern Washington and from southwestern Montana and southern Idaho southward to west-central Colorado and southern Idaho (Fig. 182). Forty specimens from 8 localities were examined.

Specimens have been collected from late May until early July. This species has the earliest flight period of those in the *E. detersa* group.

Habitat. No available data.

Remarks. Specimens of *E. melura* are similar in wing markings to those of *E. olivalis*. Specimens of *E. melura* can usually be distinguished from those of *E. olivalis* by the rounded orbicular spot and by earlier collecting date. Specimens of the two species are easily distinguished by genitalia. Males of *E. melura* have short sacculus extensions and long harpes; those of *E. olivalis* have long sacculus extensions and short harpes. Ovipositor valve of *E. melura* female has stout setae apically; that of *E. olivalis* female has fine setae and a sclerotized flange at apex.

3.4.29. *Euxoa detersa* (Walker)

Figs. 60, 61, 93, 123, 155, 183, 198

Charaeas detersa Walker, 1856, p. 212; Nova Scotia.

Agrotis detersa; Grote, 1873, p. 82.

Carneades detersa; Smith, 1893, p. 94.

Paragrotis detersa; Dyar, 1902, p. 142.

Euxoa detersa; Hampson, 1903, p. 229.

Euxoa detersa; Draudt, 1924, p. 40; redescription.

Euxoa detersa; McDunnough, 1949, p. 3.

Euxoa detersa; McDunnough, 1950, p. 371; redescription.

Agrotis detersa; Forbes, 1954, p. 38.

Euxoa detersa; Rings and Johnson, 1976, 1-16; bibliography.

Agrotis pitychrous Grote, 1873, p. 82; Long Island, New York.

Carneades pitychrous; Smith, 1890b, p. 159; redescription.

Carneades pitychrous; Smith, 1893, p. 94; = *E. detersa*.

Agrotis personata Morrison, 1876, p. 238; Illinois.

Agrotis personata; Grote, 1880a, p. 187; = *E. pitychrous*.

Carneades personata; Smith, 1890b, p. 159; = *E. pitychrous*.

Paragrotis personata; Dyar, 1902, p. 142; = *E. pitychrous*.

Euxoa personata; Hampson, 1903, p. 229; = *E. pitychrous*.

Euxoa personata; Smith, 1910a, p. 106; good species.

Euxoa detersa personata; Barnes and McDunnough, 1917, p. 41.

Euxoa detersa personata; Draudt, 1924, p. 40; redescription.

Agrotis personata; Forbes, 1954, p. 38; good species.

Euxoa detersa personata; Lafontaine, 1980.

Agrotis azif Strecker, 1898, p. 6; Clyde, New York.

Paragrotis azif; Dyar, 1902, p. 143.

Euxoa detersa azif; Barnes and McDunnough, 1917, p. 41.

Euxoa detersa personata form *azif*; Draudt, 1924, p. 40.

Euxoa detersa azif; McDunnough, 1938, p. 58.

Euxoa azif; Lafontaine, 1980; = *E. detersa personata*.

Description. Frontal tubercle markedly reduced, absent in many specimens. Vestiture of head and thorax gray and brown. Ground color of forewing pale gray, buff or brown. Basal and subterminal areas slightly paler than median area in some specimens. Terminal area gray-brown, darker than ground color of forewing. Reniform and orbicular spots slightly paler than median area. Claviform spot black, inconspicuous. Costa and veins Cu, Cu_1 and M_3 pale-lined and pale streak distal to claviform spot in most specimens from Atlantic seaboard and lower St. Lawrence River region. Hind wing of male varied from buff basally with smoky-brown shading on outer third of wing to entirely smoky-brown. Hind wing of female smoky-brown.

Expanse: 30.6±1.2 mm. Length of forewing: 15.3±0.8 mm (100 specimens).

Male genitalia (Fig. 93). Harpe markedly curved toward valve mesially and apically. Sacculus invaginated at base of clavus; clavus large, sclerotized. Vesica without extra nipple-like subbasal diverticulum and without basal bulge on median diverticulum.

Length of right sacculus extension: 1.43±0.11 mm (23 specimens).

Length of left sacculus extension: 1.31±0.12 mm (23 specimens).

Length of right harpe: 1.08±0.06 mm (23 specimens).

Length of right sacculus: 1.30±0.07 mm (23 specimens).

Female genitalia (Figs. 123, 155). Corpus bursae oval, slightly invaginated on left side. Ovipositor valve with stout setae dorsally and apically; stout setae scattered on dorsal margin of valve, not in a row. A few long setae on ovipositor valve sub-basally but no row of long sub-basal setae.

Type material. *Charaeas detersa* Walker was described from four specimens; these are in the collection of the British Museum (Natural History). A male labelled "type", "Nova Scotia", "2. *Charaeas* ? *detersa*", "Noctuidae, Brit. Mus. slide No. 6307", is here designated lectotype.

Agrotis pitychrous Grote was described from an unknown number of specimens from Long Island, New York. Type material, stated to be in the Lintner collection, now deposited in the collection of the New York State Museum, Albany, has not been located. Characters given in the original description, however, are sufficient to allow the names *E. detersa* and *E. pitychrous* to be synonymized.

The nominal holotype of *Agrotis personata* Morrison is a female in the collection of Michigan State University, East Lansing. The origin of the holotype was stated to be Illinois, however, the specimen is labelled "Ohio".

The holotype of *Agrotis azif* Strecker is a female in the collection of the Field Museum of Natural History, Chicago.

Distribution and period of flight. *Euxoa detersa* occurs on the Atlantic seaboard from Gaspé Peninsula, Quebec southward to South

Carolina. Its range extends westward through the St. Lawrence River region and the Great Lakes region to the Great Plains. In central North America E. detersa occurs from north-central Manitoba and south-central Alberta southward to southern Minnesota and central Nebraska. It has also been collected at Fort Smith, Northwest Territories (Fig. 183). Reports of this species from Colorado (e.g. Forbes, 1954) are apparently based on misidentified specimens of E. cinereopallida (Smith), and on mislabelled specimens of the Atlantic seaboard form of E. detersa. Approximately 1000 specimens from 105 localities were examined.

Specimens have been collected from early August until early October.

Habitat. This species inhabits areas of loose, shifting sand such as beach and dune areas.

Remarks. Specimens of E. detersa may be distinguished from those of E. cicatricosa by characters in key (see also remarks under E. cicatricosa).

The larva of E. detersa is commonly called the sandhill cutworm. It is a locally important economic pest of crops grown in sandy soil including corn, tobacco, potatoe, strawberry, oats, wheat and rye (Rings and Johnson, 1976).

Populations of E. detersa may be arranged in two subspecies as follows:

Euxoa detersa detersa (Walker)

Charaeas detersa Walker, 1856, p. 212.

Agrotis pitychrous Grote, 1873, p. 82.

The nominate subspecies occurs in eastern North America from the Atlantic seaboard westward in the St. Lawrence River region as far west as the eastern Great Lakes region.(Fig. 198). In most specimens of this subspecies the forewing is streaked longitudinally with costa, and veins Cu, Cu_1 and M_3 pale-lined; the claviform spot has a pale streak distal to it (Fig. 60).

Euxoa detersa personata (Morrison)

Agrotis personata Morrison, 1876, p. 238.

Agrotis azif Strecker, 1898, p. 6.

This subspecies occurs from central North America eastward through the Great Lakes region to the St. Lawrence River region (Fig. 198). In specimens of this subspecies the forewing is not streaked longitudinally (Fig. 61).

Specimens from the upper St. Lawrence River region, the Ottawa Valley and upper state New York are extremely varied; both streaked and non-streaked forms occur as well as every combination of forms between these two extremes.

3.4.30. *Euxoa cicatricosa* (Grote and Robinson)

Figs. 62, 63, 94, 124, 156, 184, 198

Agrotis cicatricosa Grote and Robinson, 1865, p. 492; Colorado.

Carneades cicatricosa; Smith, 1890b, p. 138; redescription.

Carneades cicatricosa; Smith, 1893, p. 88; catalogue.

Paragrotis cicatricosa; Dyar, 1902, p. 140.

Euxoa cicatricosa; Hampson, 1903, p. 205.

Euxoa cicatricosa; Draudt, 1924, p. 37; redescription.

Euxoa cicatricosa; McDunnough, 1949, p. 3.

Carneades neomexicana Smith, 1890b, p. 218; New Mexico.

Carneades neomexicana; Smith, 1893, p. 88; catalogue.

Paragrotis neomexicana; Dyar, 1902, p. 140.

Euxoa neomexicana; Hampson, 1903, p. 206.

Euxoa cicatricosa neomexicana; Barnes and McDunnough, 1917, p. 41.

Euxoa cicatricosa neomexicana; Draudt, 1924, p. 37; redescription.

Carneades neomexicana; Rindge, 1955, p. 122; type material.

Euxoa neomexicana; Lafontaine, 1970; = *E. cicatricosa*.

Setagrotis ducalis Smith, 1907, p. 128; Stockton, Utah.

Euxoa ducalis; Barnes and McDunnough, 1917, p. 41.

Euxoa ducalis; Draudt, 1924, p. 37; redescription.

Euxoa ducalis; McDunnough, 1925, p. 244; near *E. olivalis*.

Euxoa ducalis; Lafontaine, 1980; = *E. cicatricosa*.

Euxoa teplia Smith, 1910b, p. 253; Colorado; Stockton, Utah.

Euxoa teplia; Barnes and McDunnough, 1917, p. 41; = *E. cicatricosa*.

Euxoa teplia; Rindge, 1955, p. 133; type material.

Description. Frontal tubercle present. Vestiture of head and thorax gray, brown, and white scales. Ground color of forewing gray-brown with pale streaks. Subterminal area, costa, reniform and orbicular spots, streak distal to claviform spot, and veins Cu, Cu_1 and M_3 silver-gray, white, or orange-brown, paler than remainder of forewing. Veins Cu_1 and M_3 pale-lined, projected into terminal area. Small, black basal dash in some specimens. Claviform spot black, small. Hind wing of male white, light buff shading near terminal margin in some specimens. Hind wing of female buff with smoky-brown shading on veins in many specimens.

Expanse: 29.8±1.4 mm. Length of forewing: 14.8±0.7 mm (100 specimens).

Male genitalia (Fig. 94). Similar to those of *E. detersa* male; most structures smaller, on average, than those of *E. detersa* male.

Length of right sacculus extension: 1.32±0.12 mm (25 specimens).

Length of left sacculus extension: 1.16±0.13 mm (25 specimens).

Length of right harpe: 0.99±0.05 mm (25 specimens).

Length of right sacculus: 1.24±0.08 mm (25 specimens).

Female genitalia (Figs. 124, 156). Similar to those of *E. detersa* female but may be distinguished from them by arrangement of stout setae on ovipositor valve. Stout setae on ovipositor arranged in a row on dorsal margin of valve.

Type material. The holotype of *Agrotis cicatricosa* Grote and Robinson is a female (type No. 7595) in the collection of the Academy of Natural Sciences of Philadelphia.

Carneades neomexicana Smith was described from "several specimens". Syntypes are in the collections of the United States National Museum and the American Museum of Natural History. A lectotype will be designated by Todd (1980).

The holotype of *Setagrotis ducalis* Smith is a female in the collection of the United States National Museum. The specimen has been dissected.

Euxoa teplia Smith was described from one male and one female. The specimens are in the collection of the American Museum of Natural History. A lectotype will be designated by Todd (1980).

Distribution and period of flight. *Euxoa cicatricosa* occurs from central Saskatchewan westward to south-central British Columbia and southward to northern Texas, southern New Mexico, central Arizona and southern California (Fig. 184). Approximately 1300 specimens from 101 localities were examined.

Specimens have been collected from late August until late October.

Habitat. *Euxoa cicatricosa* occurs in very arid areas where vegetation is sparse and soil is loose, coarse sand or gravel.

Remarks. Specimens of *E. cicatricosa* are similar to those of *E. niveilinea* in wing markings and color. Males of *E. cicatricosa* may be distinguished from those of *E. niveilinea* by shorter sacculus extension of the genitalia; females may be distinguished by stout setae rather than sclerotized flange on ovipositor valve. Most specimens of *E. cicatricosa* can be distinguished from those of *E. niveilinea* by lack of transverse white band on thorax posterior to prothoracic collar and by presence of a pale streak distal to claviform spot on forewing.

In structural characters, E. cicatricosa specimens are most similar to those of E. detersa and E. recula. Stout setae on ovipositor of E. cicatricosa female form a single row on dorsal margin of valve; these setae are scattered on dorsal margin of valve, not in a row, in females of E. detersa and E. recula.

Specimens of E. cicatricosa may be distinguished from those of E. recula by pattern and color of forewing. In specimens of E. cicatricosa the forewing is dark gray-brown with fine silver-gray streaks. Reniform and orbicular spots have dark central spots. In specimens of E. recula, pale areas of forewing are more extensive and are yellow. Reniform and orbicular spots and a broad streak extended from claviform spot to subterminal line are yellow.

Most specimens of E. cicatricosa may be distinguished from those of E. detersa personata by presence of longitudinal streaks on the forewing, particularly pale-lined veins Cu_1 and M_3 projected into terminal area and by pale hind wing. A form of E. cicatricosa occurs at some localities in the Great Plains, particularly in south-central Saskatchewan, with the forewing not longitudinally streaked. Forewings of these specimens are similar to those of E. detersa specimens from the same region and these specimens may be the result of hybridization. In other characters, however, the specimens are not intermediate; setal arrangement on ovipositor valves, hind wing color, and frontal tubercle size are normal for E. cicatricosa specimens. Similar unstreaked forms also occur in Texas, Kansas and Colorado outside of the known range of E. detersa.

Euxoa cicatricosa specimens are varied in wing markings. The most widespread form (Fig. 63) occurs throught the range of the species except for the Great Basin and southwestern United States. A pale form, with more extensive white streaks (Fig. 62) occurs in the Great Basin. Pale markings on specimens from New Mexico and Arizona are orange-brown rather than white or silver-gray.

3.4.31. Euxoa recula (Harvey)

Figs. 64, 95, 125, 157, 185, 198

Agrotis recula Harvey, 1876, p. 37; Oregon.

Carneades recula; Smith, 1890b, p. 138; redescription.

Carneades recula; Smith, 1893, p. 88; catalogue.

Paragrotis recula; Dyar, 1902, p. 140.

Euxoa recula; Hampson, 1903, p. 207; redescription.

Euxoa cicatricosa recula; Barnes and McDunnough, 1917, p. 41.

Euxoa cicatricosa recula; Draudt, 1924, p. 37; redescription.

Euxoa recula; Lafontaine, 1980; good species.

Description. Frontal tubercle present. Vestiture of head and thorax yellow-buff and gray scales. Ground color of forewing brownish gray with extensive yellow shading. Basal and subterminal areas, costa, reniform and orbicular spots, and area distal to claviform spot shaded with yellow in most specimens. Some specimens with silver-gray shading on costa and in subterminal area. Veins Cu, Cu_1 and M_3 pale-lined, latter two projected into subterminal area. Hind wing of male white; hind wing of female pale buff with smoky-brown shading on veins.

Expanse: 30.8±1.5 mm. Length of forewing: 15.4±0.7 mm (100 specimens).

Male genitalia (Fig. 95). Similar to those of E. detersa and E. cicatricosa males but most structures, on average, smaller.

Length of right sacculus extension: 1.12±0.12 mm (20 specimens).

Length of left sacculus extension: 1.02±0.12 mm (20 specimens).

Length of right harpe: 0.92±0.04 mm (20 specimens).

Length of right sacculus: 1.20±0.04 mm (20 specimens).

Female genitalia (Figs. 125, 157). Indistinguishable from those of *E. detersa* female. May be distinguished from those of *E. cicatricosa* female by arrangement of stout setae on dorsal margin of ovipositor valve, these scattered, not in a single row as in *E. cicatricosa* female.

Type material. *Agrotis recula* was described by Harvey from two females collected in Oregon. One of these has been located in the collection of the British Museum (Natural History). The specimen, labelled "type", "Oregon, Grote Coll. 81-116", "5969 Oregon", "*Agrotis recula* Harvey", "*Agrotis recula* Harvey type", "Noctuidae, Brit. Mus. slide No. 6359", is here designated lectotype. The specimen is a female in fair condition.

Distribution and period of flight. *Euxoa recula* occurs from central Oregon southward to southern California and westward through southern Arizona to central New Mexico (Fig. 185). Approximately 400 specimens from 32 localities were examined.

Specimens have been collected from early September until late October.

Habitat. *Euxoa recula* occurs in habitats similar to those inhabited by *E. cicatricosa*. The two species are frequently collected together in Nevada and Oregon. In southern Arizona and in the Mojave Desert, California, however, *E. recula* is found in areas where *E. cicatricosa* does not occur.

Remarks. Specimens of *E. recula* may be distinguished from those of *E. cicatricosa* and *E. detersa* by characters in key (see also remarks under *E. cicatricosa*).

4. Phylogeny

4.1. Introduction

The following chapter presents a discussion of two phylogenies, one of the subgenera and species groups of *Euxoa* (Fig. 199), and one of the species of the *E. detersa* group (Fig. 200). Construction of both phylogenies was based on Hennigian principles as outlined by numerous recent workers (e.g. Schlee, 1969; Kavannaugh, 1972; Whitehead, 1972; Munroe, 1974) by establishing sister group relationships on the basis of shared, derived character states (synapomorphies of Hennig, 1966). Morphological uniformity among *Euxoa* species, and extensive intraspecific variability frequently made it necessary to characterize groups on the basis of overall similarity and group trends. This parallels the situation described by Whitehead (1976) for the weevil genus *Rhinochenus*.

Before attempting a phylogenetic reconstruction of the *E. detersa* group, it was necessary to trace character states and trends through the rest of the genus in order to determine ancestral and derived conditions in the *E. detersa* group and to evaluate their usefulness for phylogenetic purposes. Such a comparison of *Euxoa* character states has not been done previously. In addition, other genera of the Noctuinae were examined to determine ancestral character states for the genus.

The structural uniformity within the family Noctuidae, especially among the assemlage of subfamilies collectively known as trifid noctuids, makes the formulation of phylogenetic reconstructions particularly difficult. Richards (1932) and Kiriakoff (1963), for example, studied the structure of the thoracic ear in an attempt to shed light on the phylogeny of the Noctuidae and related families. They were, however, unable to find any characters that would aid in distinguishing the 'trifid' subfamilies. Phylogenies have been constructed for the genera of the Noctuinae (Forbes, 1933); Stiriini (Hogue, 1963); Heliothidinae (Hardwick, 1970b); and Plusiinae (Eichlin and Cunningham, 1978).

Alternatives to a strictly morphological approach to phylogenetic reconstruction in the noctuids have barely been considered. The possibility of using serological studies of proteins was investigated by Martin and Cotner (1934) and discussed by Hudson (1973). Although the results of these investigations seem promising, a more critical and comprehensive study has not been made.

4.2. Relation of Euxoa to other noctuine genera

In a revision of the genera of the Agrotinae (=Noctuinae), McDunnough (1928) stated that Euxoa was most closely related to Protexarnis, Loxagrotis, and Pseudorthosia, although he did not include a detailed phylogeny. Forbes (1933), using a phenetic approach to reconstruct a phylogeny for the Noctuinae, provided the most reasonable hypothesis of the phyletic position of Euxoa in the subfamily. Forbes considered Peridroma to be the genus retaining the largest number of ancestral character states within the Noctuinae. This position is further supported by the work of Birch (1972a, 1972b) on British noctuids who found that Peridroma is the only genus in the Noctuinae that has retained male abdominal scent-brushes.

According to Forbes' hypothesis, a Peridroma-like ancestor gave rise to two lineages, one in which the fore-tibial setae of adults were progressively reduced, and one in which they were enlarged into digging claws. Also in this latter group, the length of the fore-tibia is reduced and the frons is modified, this usually either bulging and roughened or with a projecting frontal tubercle. These three derived character states are related to the subterranean pupation habit of the larvae, apparently being adaptations that aid the adults in escaping from the soil upon emergence. Genera belonging to this group include Euxoa, Agrotis, Feltia, and Loxagrotis. Ancestral character states of these genera are: male antennae biserrate and bifasciculate; juxta with a projecting spine; male valve with sacculus large; sacculus with an apical bulge; digitus present on cucullus; harpe short, projected dorsally; vesica with one or more cornuti near base; female with bursa copulatrix bisaccate (i.e. cervix bursae present, see Callahan and Chapin, 1960); ovipositor valves without stout setae or sclerotized projections. According to Forbes, *Euxoa* is the sister group of a large number of genera (e.g. *Agrotis*, *Feltia*, *Loxagrotis*) that share the same tarsal and frontal modifications as *Euxoa*. Although Forbes does not mention which characters were used in reconstructing this phylogeny, the shared, derived character state of *Euxoa* is development in males of a sacculus extension projected along the ventral edge of the cucullus. Also the digitus on the cucullus is lost in *Euxoa*. A shared, derived character state of the sister group of *Euxoa* is a long, sclerotized projection extended onto the vesica from the apex of the aedeagus. Males of most genera of this group, however, are more easily recognized by the position and shape of the harpe, which is reduced and is extended along the inner surface of the cucullus. The female genitalia, not used by Forbes, offer excellent derived character states for these two lineages. The ancestral condition of the ductus bursae is one in which the walls are sclerotized and form a sheath. The sclerotized portion varies from occupying the posterior third to extending almost the full length of the ductus. In the female genitalia of *Euxoa* the sclerotized portion is reduced to two plates, one in the dorsal wall and one in the ventral wall of the ductus. In females of the sister group of *Euxoa* the ductus bursae is membranous.

Fletcher (1961) considered the African genus Euxootera to be closely related to Euxoa. This assumption, however, is based primarily on the presence of a sacculus extension in males. This represents a situation similar to that of Protexarnis which was discussed by Forbes (1933). Lack of tarsal and frontal modifications in adults of these genera suggests that the sacculus extensions are convergent with those of Euxoa males.

4.3. Phylogeny of species groups of *Euxoa*

The ancestral character states for the genus are: those of the ancestral states of the *Euxoa* group of genera (see above) plus, male genitalia with uncus tapered to apex; sacculus extension short and rounded; harpe without pubescence; vesica curved in a loop above apex of aedeagus to project dorsally; vesica with a single sub-basal diverticulum.

Reconstruction of a phylogeny of *Euxoa* was difficult and results must be considered tentative. Three major problems encountered were structural uniformity of the species, extensive parallelism in some character states, and scattered distribution of a number of derived character states. Many of the character states used are not discrete derived character states but are similarities in shape and proportion created by modifications of a number of genitalic structures. Species groups were combined on the basis of shared, derived character states into progressively more inclusive lineages until all species groups were included in the phylogeny.

The structures and the distribution of derived character states among the subgenera and species groups of *Euxoa*, which are used in the phylogenetic analysis, are shown in table 1.

Table 1. Structures and Evolutionary Classification and Distribution of Character States among Subgenera and Species Groups of Euxoa.

Structure/ Character	Ancestral State	Derived State	Basis for Classf'n	Times derived	Times lost	Distribution of derived state by lineage (Fig. 199)
1 Antenna of male	biserrate	a) plumose	Ex.	2 (3?)	-	4•, 5, 6
		b) filiform	Ex.	2	-	1, 13•
2 Frontal tubercle	present	absent	Ex.	3	-	4•, 11, 12•
3 Uncus	apically narrow	apically spatulate	Ex.	1 (2?)	- (1?)	13•
4 Juxta spine	present	absent	Ex.	1	-	2-13
5 Sacculus	large	reduced	Ex. In.	6	-	2•, 4•, 5, 6, 9•, 11-13
6 Sacculus extension	short, spatulate	a) elongate, cylindrical	Ex. In.	1	8 (see b & c)	3, 4•, 7, 8, 9•, 10•, 11, 12, 13•
		b) short, cylindrical	Ex. In.	6	-	4•, 5, 6, 13•
		c) flattened, blade-like	Ex. In.	2	2	9•, 10•
7 Harpe - length	short	elongate	Ex.	2	-	2•, 3-13
8 Harpe - pubescence	absent	present	In.	1	6	9•,10,11•,12•,13•

Table 1 Continued

9	Vesica loop	present	absent	Ex.	4	-	1, 3•, 4-13
10	Vesica - 2nd sub-basal diverticulum	absent	present	Ex. In.	127	7	5, 6, 8•, 9•, 10•, 11•, 12•, 13•
11	Vesica - cornuti	present	absent	Ex. In.	14	-	1, 2, 3•, 4•, 5, 6, 7•, 8•, 9•, 10•, 11•, 12•, 13•
12	Bursa	bisaccate	unisaccate	Ex. In.	8	-	1, 3•, 4•, 9•, 10•, 11•, 12-13
13	Ovipositor flanges	absent	present	Ex. In.	1	18	10•, 11•, 12•, 13•
14	Ovipositor flanges	not fused	fused	Ex. In.	5	-	10, 11•, 13•
15	Ovipositor with sclerotized rim	absent	present	Ex.	1	1	9•
16	Ovipositor with stout setae	absent	present	Ex.	3	-	4•, 12•

Explanation of symbols and abbreviations used:
• - not present in all taxa
Ex. - ex-group comparisons
In. - in-group comparisons

4.3.1. Parallelism and secondary losses

The structural uniformity among Euxoa species presents a serious obstacle to phylogenetic analysis. Many of the derived character states listed in table 1 are changes in shape or size and are susceptible to parallel evolution. For example, trends toward a reduction in the size of the sacculus and a reduction in the length of the sacculus extension occur independently in a number of lineages.

Some character states are restricted to a lineage but are not found in all species groups of the lineage, nor are they restricted to a monophyletic grouping within it. Apparently, a number of character states (e.g. # 6, 8, 13) have been derived only once but have subsequently been lost a number of times.

Other character states, such as presence of a second sub-basal diverticulum on the male vesica, are present in a number of species groups but cannot be homologized from group to group. As a result, it has not been possible to determine how many times this character state has been derived and whether or not it has been lost secondarily by some species groups.

In spite of the hazards of using characters susceptible to parallelism and secondary loss, the groupings obtained appear to be monophyletic. Evidence of this was discovery of additional characters and trends that were revealed by grouping taxa not formerly associated. An example of this was discovery of the value of the shape and setal arrangement of the male uncus as useful taxonomic and phylogenetic characters.

4.3.2. Interpretation of character states

Some of the character states and trends listed in table 1 are explained as a necessary antecedent for reviewing the reconstructed phylogeny of subgenera and species groups shown in figure 199.

Frontal tubercle (character 2). The frontal tubercle has been lost three times, each in species associated with sandy areas.

Uncus (character 3). An apically spatulate uncus has either been derived independently in the E. cinereopallida-E. mitis lineage and the E. luctuosa group, or, more probable, it has been derived once, in their common ancestor, and lost in Orosagrotis.

Sacculus extension and harpe (characters 6 & 7). A form of the male valve, which converges on the Agrotis-like condition, with the harpe along the inner surface of the cucullus parallel to its dorsal margin and with the sacculus extension reduced has been derived three times: lineage 5; lineage 6 (E. edictalis group of Pleonectopoda); and lineage 13 (E. cinereopallida-Orosagrotis lineage).

Vesica loop (character 8). The loop in the vesica has been lost four times (lineages 1, 3, 4, 5-13), each time in a different way.

Vesica - second sub-basal diverticulum (character 10). A second sub-basal diverticulum is present in the vesica in thirteen species groups of subgenus Euxoa. The second diverticulum is a useful phylogenetic structure within species groups. It is, however, of little use for intergroup relationships because the shape and position of the diverticulum differs between groups and cannot be homologized.

Vesica - cornuti (character 11). Loss of the cornuti from the vesica is not a useful character state for phylogenetic groupings. Cornuti have been lost in fourteen species groups and in most others, their presence or absence varies from species to species and often from specimen to specimen.

. Vesica shape (not in table). The most useful phylogenetic character for associating species and species groups is the overall shape of the vesica. The shape is usually constant within a species group; species-specific characters of the vesica normally involve shape and position of the accessory pouches, primarily the sub-basal diverticulum.

Bursa (character 12). Shape of the bursa copulatrix is a very useful phylogenetic character. A unisaccate bursa (i.e. cervix bursa lost) has been derived eight times. A unisaccate bursa which is constricted mesially with the ductus bursae entering the corpus bursae at the posterior end has been derived four times: lineage 1; lineage 3 (E. olivia group); lineage 6; and lineage 9 (E. tessellata-E. choris groups). This type of unisaccate bursa probably evolved from a bisaccate type similar to that of lineage 5 (compare bursa of E. camalpa and that of E. serotina in Lafontaine, 1976b). An oval unisaccate bursa in which the ductus bursae enters the corpus bursae on the right side has been derived four times: lineage 4 (in E. westermanni group of Pleonectopoda); lineage 9 (E. rufula-E. terrena groups); lineage 10 (E. pallipennis group); and lineages 12 and 13.

Ovipositor flanges (character 13). Sclerotized flange-like projections are present on the ovipositor valves in nineteen species groups of the subgenus Euxoa (lineages 10-13), and in its derivative

Orosagrotis. The limited distribution of this structure within Euxoa and its restriction to this genus suggests that it was derived only once, this being in the common ancestor of lineages 10-13. Within these lineages, the flange-like structure has been lost many times and probably reacquired occasionally. This structure is apparently quite plastic, its presence or absence being related to oviposition habits.

Ovipositor with sclerotized rim (character 15). This character state is found only in the E. rufula-E. serricornis lineage; it has been secondarily lost in E. rufula and E. intrita.

4.3.3. Phylogeny of the genus *Euxoa*

The following is a brief explanation of the phylogeny presented in figure 199[1]. A detailed survey of the distribution of character states in the genus will not be made, nor will an attempt be made to justify all branching points in the phylogeny. An evolutionary classification, and distribution by lineage, of the character states used in the following discussion is given in table 1. The purpose of this section is to establish a rough working hypothesis of the phylogeny of the genus in order to put character states used in the phylogeny of the *E. detersa* group into perspective, and to show the relationship of the *E. detersa* group to the other species groups.

Dichotomy 1. The shared, derived character states of lineage 1 are the unique shapes of the female corpus bursae and the male vesica (see Hardwick, 1970a). Lineages 2-13 share the derived state of character 4.

Dichotomy 2. Lineage 2, while one of the most easily distinguished groups in the genus (see Lafontaine, 1975a), is difficult to define in terms of uniquely derived character states because of the large number of ancestral character states retained by its members. Structurally, species in this group are more similar to the hypothetical common ancestor of the genus than those of any other group. The shape of the bursa copulatrix in females of this lineage is unlike that of females in any other species group. Lineages 3-13 share the derived state of characters 6a and 7.

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[1] It will eventually be necessary to create a subgenus for both lineage 2 and 3. This would result in the genus consisting of six monophyletic subgenera with the subgenus *Euxoa* remaining paraphyletic with respect to the very distinctive subgenus *Orosagrotis*.

Dichotomy 3. The shared, derived character state of lineage 3 is the asymmetrical valves of the male genitalia (see Lafontaine, 1976d). Lineages 4-13 share the derived character state of having lost the loop in the vesica. This has occurred independently in lineage 1 and lineage 3 (E. olivia and E. septentrionalis groups).

Dichotomy 4. The loss of the vesica loop in the remaining subgenera and species groups (lineages 4-13) has occurred in one of two ways. The vesica has a submedian twist or coil in males of the subgenus Pleonectopoda and ancestrally in Longivesica males (see Hardwick (1970a). In Longivesica this is still evident in males of the E. divergens group. In the subgenus Euxoa (as restricted above) and Orosagrotis, the vesica has a simple bend sub-basally without a loop or twist in it.

Dichotomies 5-8. Within the subgenus Euxoa, the affinities of four lineages remain uncertain with presently available information. The remaining lineages (9-13) have been associated on the basis of the pubescence on the harpe (character 8). Although this character state is present in less than one-third of the species groups of lineages 9-13, its restriction to members of the subgenus Euxoa suggests that it has been derived only once. On this admittedly tenuous basis, lineages 9-13 are considered to form a monophyletic group.

Dichotomy 9. The species within lineage 9 share a number of uniquely derived character states but none of these is exhibited by all species groups. A markedly incurved C-shaped harpe is found in most species groups and is therefore probably a shared, derived character state of this lineage. Other derived character states are: a basally enlarged sacculus, this tending to be teardrop-shaped in males of the *E. declarata-E. simulata* lineage rather than crescentic as in males of other species groups; the sub-basal diverticulum of the vesica, rather than being elbowed and foot-shaped, is T-shaped in males of the *E. rufula-E. setonia* lineage. Another character state uniquely derived in lineage 9 is the presence of a sclerotized rim around the posterior margin of the ovipositor valve (character 15). This is found in females of the *E. rufula-E. serricornis* lineage but has been lost in females of the otherwise structurally similar *E. rufula-E. intrita* lineage. The bisaccate bursa copulatrix has been lost from females of the *E. rufula-E. terrena* lineage. Lineages 10-13 share the derived state of character 13. This has been lost independently at least eighteen times.

Dichotomy 10. Derived character states of lineage 10 are the shape of the vesica and the derived state of character 6c. Lineages 11-13 share the derived state of character 5.

Dichotomy 11. Members of lineages 11-13 have descended from a common ancestor with a bisaccate bursa copulatrix which was probably similar in shape to that found in females of the *E. punctigera* group (see Lafontaine, 1974c). A simple reduction of the cervix bursae (the left sac) resulted in the corpus bursae (the right sac) being oval, or oblong, with the ductus bursae entering it at about one-third of the way along the right side from the posterior end. This type of bursa characterizes females of lineages 12 and 13, and independently, females of the *E. pallipennis* group. A modified type of bisaccate bursa copulatrix characterizes females of the *E. obeliscoides*-*E. basalis* lineage of lineage 11 in which the corpus bursae is enlarged at each end giving it a dumbbell, or figure 8 appearance (see Hardwick, 1973a, 1973b, and Hardwick and Lefkovitch, 1973). Reduction of the cervix bursae would result in a unisaccate bursa copulatrix that is very different in shape from that which characterizes females of lineages 12 and 13. In females of the *E. tessellata*-*E. albipennis* lineage the corpus bursae appears swollen posteriorly; the ductus bursae enters at the posterior end. In females of lineages 12 and 13 the corpus bursae is oval; the ductus bursae enters the corpus bursae on the right side. An exception to this is that the corpus bursae is oval in females of the *E. albipennis* group. This group is included in lineage 11 on the basis of characters of the male genitalia.

Lineage 11 is also characterized by derived group trends in the male genitalia. The sacculus tends to be reduced, the cucullus lengthened and the apical portion of the cucullus enlarged and foot-shaped, frequently with a well developed 'heel' at the posteroventral corner. The apical two-thirds of the harpe tends to be straight rather than evenly incurved or S-shaped.

Dichotomy 12. Within lineages 12 and 13, the most difficult group to characterize in terms of uniquely derived character states is lineage 12 (the *E. detersa* group). In lineage 13, the sacculus extension is reduced in males of most species, being much shorter than the harpe. In females of lineage 13, the sclerotized flanges on the ovipositor valves tend to be fused together. In males of the *E. cinereopallida*-*Orosagrotis* lineage the harpe is along the inner surface of the cucullus. This character state, together with reduction of the sacculus extension, converges on the form of the valve characteristic of males of *Agrotis* and *Feltia*. Another derived character state of males of the *E. cinereopallida*-*Orosagrotis* lineage, but lost from *Orosagrotis* males, is an apically swollen uncus. In females of the *E. luctuosa* group, the ductus seminalis has shifted anteriorly to the middle of the left side of the corpus bursae (see Lafontaine, 1976c). This trend is continued in *Orosagrotis* females with the ductus seminalis arising at the anterior end of the bursae (*E. wilsoni* group), or on the right side (*E. ridingsiana* group) (see Hardwick, 1970a).

Lineage 12 (the *E. detersa* group), on the other hand, is characterized by the lack of the derived character states and trends described above for lineage 13. It is possible then, that the *E. detersa* group is paraphyletic in that lineage 13 may have evolved from a lineage within the *E. detersa* group.

Although many details of the phylogeny presented in figure 199 have been omitted, the above discussion is sufficient to elucidate the position of the *E. detersa* group within the genus and to allow ancestral character states to be inferred.

4.4. Phylogeny of the Euxoa detersa group

Ancestral character states for adults of the E. detersa group are: maculation normal (i.e. transverse lines all present, longitudinal streaking absent); male antenna moderately biserrate; frontal tubercle present; male genitalia with sacculus extension about 1.25 times length of harpe; vesica with single sub-basal diverticulum, this containing several cornuti, and with median diverticulum situated about one-third of way from sub-basal bend to apex; female genitalia with ovipositor valve clothed with fine setae, a sclerotized flange at apex of each valve, and a row of long setae sub-basally; ductus bursae entering corpus bursae on right side about one-third of way from posterior end.

The 31 species in the E. detersa group are easily arranged in 12 monophyletic lineages (see figure 200) on the basis of both structural and wing marking similarity. Many of the species within these lineages are distinguished only by numerical techniques or subtle differences in wing markings. Most of these lineages were defined and grouped into more inclusive monophyletic units on the basis of discrete, shared, derived character states. Unfortunately, structural uniformity within the E. detersa group made it necessary to associate some lineages on the basis of overall structural similarity.

Structures and distribution of derived character states used in the phylogenetic analysis of the E. detersa group are shown in tables 2 and 3.

Table 2. Structures and Evolutionary Classification and Distribution of Character States among Adults of the Euxoa detersa Group.

Structure/ Character	Ancestral State	Derived State	Basis for Classf'n	Times derived	Times lost	Distribution of derived state by lineage (Fig. 200)
1 Wing markings	unstreaked	streaked	Ex. In.	4	-	1-2, 3*, 4, 8-12
2 Sexual dimorphism	absent	present	Ex.	1	-	8
3 Antenna of male	biserrate	slightly biserrate	Ex.	1	-	7*
4 Uncus setae	not stout mesially	stout mesially	Ex.	1	-	7*
5 Clavus	small	enlarged	Ex.	1	-	12
6 Vesica projection	dorsal	lateral	Ex.	1	1	1, 3
7 Vesica - twist in sub-basal bend	absent	present	Ex.	1	-	2
8 Vesica - 2nd sub-basal diverticulum	absent	present	Ex. In.	1	5	6, 7*, 8*, 10, 11
9 Vesica - median diverticulum	near basal bend	mesial	Ex.	1	-	1, 2

Table 2 Continued

10	Vesica - median diverticulum	no basal bulge (see text)	basal bulge	Ex.	1	2	7-10, 11*
11	Vesica - cornuti	present	absent	Ex.	1	-	3
12	Ovipositor flange	present	absent	Ex.	5	2	1, 2, 3*, 7*, 8*, 11-12
13	Ovipositor - conical setae	absent	present	Ex.	1	-	1
14	Ovipositor- stout setae apically	absent	present	Ex.	2	-	3*, 11-12
15	Ovipositor - stout basal setae	absent	present	Ex.	1	-	11
16	Ovipositor - enlarged ventrally	absent	present	Ex.	1	-	5
17	Ductus bursae entering corpus bursae	posteriorly	mesially	Ex.	1	-	1-5
18	Corpus bursae	elongate	rounded	Ex.	1	-	4

Table 3. Distribution of Derived Character States among Adults of the *Euxoa detersa* Group.

Lineage No.	Species	Fig. No.	Character State Number (see table 2)										
						Male Genitalia							
			1	2	3	4	5	6	7	8	9	10	11
1	costata	65	x					x			x		
	castanea	66	x					x			x		
	foeminalis	67	x					x			x		
	idahoensis	68	x					x			x		
	clausa	69	x					x			x		
2	brevipennis	70	x					-	x		x		
3	servita	71	x					x					x
	redimicula	72						x					x
	auripennis	73						x					x
	arizonensis	74						x					x
4	olivalis	75	x										
	agema	76	x										
	oblongistigma	77	x										
5	citricolor	78											
	tronella	79											
6	teleboa	80								x			
7	moerens	81			x	x				x		x	
	latro	82			x	x				x*		x	
	murdocki	83			x	x				-		x	
	dodi	84								-		x	
	infracta	85								-		x	
8	laetificans	86	x	x						x		x*	
	quadridentata	87	x	x						-		x	
9	inscripta	88	x							-		x	
	unica	89	x							-		x	
10	niveilinea	90	x							x		x	
11	dargo	91	x							x		x	
	melura	92	x							x		-	
12	dargo	93	x*				x			-		-	
	cicatricosa	94	x				x			-		-	
	recula	95	x				x			-		-	

* = not present in all specimens

- = derived character state secondarily lost

Table 3 Continued

Lineage No.	Species	Fig. No.	Character State Number (see table 2)						
			Female Genitalia						
			12	13	14	15	16	17	18
1	costata	96, 126	x	x				x	
	castanea	97, 127	x	x				x	
	foeminalis	98, 128	x	x				x	
	idahoensis	99, 129	x*	x				x	
	clausa	100, 131	x	x				x*	
2	brevipennis	101, 132	x					x*	
3	servita	102, 133	x		x			x	
	redimicula	103, 134						x	
	auripennis	104, 135						x	
	arizonensis	105, 136						x	
4	olivalis	106, 137						x	x
	agema	107, 138						x	x
	oblongistigma	108, 139						x	x
5	citricolor	109, 140					x	x	
	tronella	110, 141					x	x	
6	teleboa	111, 142							
7	moerens	112, 143							
	latro	113, 144							
	murdocki	114, 145							
	dodi	115, 146	x						
	infracta	116, 147	x						
8	laetificans	117, 150	x						
	quadridentata	118, 148	x*						
9	inscripta	119, 151							
	unica		? (♀ unknown)						
10	niveilinea	120, 152							
11	dargo	121, 153	x		x	x			
	melura	122, 154	x		x	x			
12	detersa	123, 155	x		x				
	cicatricosa	124, 156	x		x				
	recula	125, 157	x		x				

* = not present in all specimens

4.4.1. Phylogeny of the lineages of the *Euxoa detersa* group

The reconstructed phylogeny of the *Euxoa detersa* group, and the numbers of characters used in grouping the lineages, are shown in figure 200. Each circled number represents one of the 12 lineages.

Early differentiation produced two stocks (lineages 1-5; and lineages 6-12), which have become almost equally diverse. In general, the pattern of character differentiation has been conservative, consisting of slight modifications (with frequent reversals) of various elements of the genitalia, in contrast to a more linear type of character modification resulting from progressive changes of a single character. Nevertheless, lineages 1-5 are linked by a modification of the bursa, and in general exhibit more modifications in the female genitalia than are exhibited by females of lineages 6-12. Conversely, lineages 6-12 are linked by modifications of the male vesica, and generally exhibit more changes in the male genitalia than are exhibited by males of lineages 1-5.

Lineages 1 and 3 share the derived character state of the vesica projected to the left rather than dorsally above the apex of the aedeagus (character 6). This is most likely a derived character state shared by lineages 1-3 that has been lost by lineage 2. The vesica of specimens of lineage 2 (*E. brevipennis*) has a slight twist in the sub-basal bend of the vesica (character 7) returning the direction of its projection to the ancestral position.

The shared, derived character state linking lineages 6-12 is presence in males of an additional, small, sub-basal diverticulum (character 8) situated dorsolaterally on the left side opposite the normal, foot-like sub-basal diverticulum. This has apparently been lost from lineages 9 and 12 and from males of some species of lineages 7 and 8.

The shared, derived character state uniting lineages 7-12 is that the median diverticulum of males has a bulge at its base and the basal half of the diverticulum is projected dorsally parallel to the axis of the vesica (character 10). This has been lost in lineage 12 and by males of *E. melura* and some specimens of *E. laetificans*. Ancestrally this diverticulum is horn-shaped and projects from the vesica at right angles.

The sequence of evolutionary changes of male vesica is shown in diagram 1 (page 169).

Lineage 7 contains adults whose forewings are not streaked longitudinally while those of lineages 8-12 are streaked (character 1). The non-streaked pattern is considered to be the ancestral condition for the *E. detersa* group since this is the pattern that predominates in the genus. A similar streaked pattern, however, does occur independently in a number of species groups. Such a pattern would be expected to arise many times since it is cryptic for individuals that rest among grasses during the day. Although the streaked and non-streaked patterns seem susceptible to parallel evolution, a dichotomy based on these does appear to be justified on the basis of the corresponding overall similarity of the genitalia of species within each group.

Lineages 8, 9 and 10 are each considered to be the sister group of the remaining lineages on the basis that after each dichotomy, species in the remaining lineages are more similar to each other in both genitalia and wing pattern.

4.4.1.1. Alternative hypotheses

Structural uniformity among species of the Euxoa detersa group presents an obvious obstacle to phylogenetic analysis. Many structural characters that are present have been independently lost or derived in several lineages, this further weakening the credibility of the reconstructed phylogeny. Considering the shortcomings of available data, it is advisable to discuss some alternative hypotheses and problem areas of the reconstructed phylogeny of the Euxoa detersa group in the hope that discovery of additional characters will shed light on these problem areas.

Problem areas in a reconstructed phylogeny can be of three types; these are: incorrect assignment of species to a lineage; incorrect reconstructed phylogeny of species within a lineage; incorrect arrangement of lineages.

The only apparent possibility of a problem of the first type is with lineage 9. The sister group relationship of species in lineage 9 would be incorrect if it could be shown that Euxoa unica McD. is not a species but the product of interspecific hybridization. This possibility is discussed in section 3.4.25.

Of the second type, problems associated with reconstructing the phylogeny of lineages 1 and 3 are discussed in section 4.4.2.

Many problems were encountered in arranging lineages into larger monophyletic groups, these resulted from a lack of characters. General appearance of wing markings and genitalia of members of lineages 2 and 5 are incongruent with those of lineages with which they have been associated. Undoubtedly some incongruency results from different habitat preferred by members of these two lineages, however, the possibility of convergence cannot be ruled out. The larger number of derived character states shared by members of lineage 2 and those of associated lineages as compared to that of members of lineage 5 makes the possibility of convergence in lineage 2 less likely than it is in lineage 5.

Arrangement of lineages 8-10 is based on increasing overall similarity of their members to those of lineages 11+12. Discovery of additional characters could change this arrangement.

In the _Euxoa_ _detersa_ group characters suitable for phylogenetic analysis are so few, and the possibility of convergent evolution so great, that discovery of additional characters could change the position of some lineages in any number of ways. For these reasons, no attempt is made to suggest where lineages discussed above would be placed in a reconstructed phylogeny after discovery of additional characters.

4.4.2. Phylogeny of the species of the *Euxoa detersa* group

Of the five lineages which include more than two species (i.e. #1, 3, 4, 7 and 12), lineage 1 presented the most difficulties in reconstruction of phylogenetic relationships. The species in this lineage are so uniform structurally that only distribution patterns, wing color and maculation can be used in reconstructing a phylogeny. *Euxoa costata* and *E. castanea* are considered sister species on the basis of the characteristic reddish-brown, or chestnut, color of the forewings. The assumption that these two species share a recent common ancestry is further supported by the distribution patterns of the two species. *Euxoa castanea* is distributed in the Rocky Mountain region while *E. costata* is distributed along the Cascade-Sierra Nevada axis, the two being sympatric only in the north-west (see figure 188). The phylogeny of the remaining three species in the lineage was constructed from more circumstantial evidence. *Euxoa clausa* and *E. foeminalis* both have restricted distributions which are contained within the distribution of *E. idahoensis*. *Euxoa idahoensis* is a widespread and polytypic species with features which are suitably ancestral for either one, whereas *E. clausa* and *E. foeminalis* are forms which would fall at opposite ends of the range of variation of *E. idahoensis*. It thus seems more likely that *E. clausa* and *E. foeminalis* are more closely related to *E. idahoensis* than to each other. *Euxoa foeminalis* is tentatively associated more closely with *E. idahoensis* than is *E. clausa* because of the similarities in wing markings.

In lineage 3 *E. servita* is considered to be the sister species of the *E. redimicula-E. arizonensis* lineage because *E. servita* is the most divergent of the four species in the lineage in terms of both genitalia structures and maculation and is sympatric with the other three species (see Lafontaine, 1974a). The three species in the *E. redimicula-E. arizonensis* lineage are largely allopatric and may be the result of trichotomous speciation. The evidence, however, suggests otherwise. Adults of *E. auripennis* and *E. arizonensis* are more similar to each other than they are to those of *E. redimicula*. It is possible that *E. arizonensis* and *E. auripennis* speciated from a common ancestor during the Wisconsinan while *E. redimicula* appears to have arisen in pre-Wisconsinan times. Both *E. auripennis* and *E. redimicula* occur in disjunct woodland areas within the Great Plains and the two may have been widely sympatric in this area during the Wisconsinan when large portions of the Great Plains were forested (see figure 190).

In the phylogeny of lineage 4, *E. agema* is considered to be the sister species of *E. oblongistigma*. Although adults of *E. agema* are more similar to those of *E. olivalis* in terms of wing markings than to adults of *E. oblongistigma*, the genitalia of males of *E. agema* and *E. oblongistigma* share the derived character state of having a shortened sacculus extension and a lengthened harpe. These structural characters probably reflect phylogenetic affinities more accurately than do wing markings.

In lineage 7, males of *E. moerens*, *E. latro*, and *E. murdocki* share a derived condition of the uncus setae. In these species, setae on the middle portion of the uncus are short and stout, and have a brush-like appearance. Normally only setae on the apical third of the uncus are stouter and these are not erect and brush-like; setae on the middle portion of the uncus are thin and hair-like. Also the antennal serrations are reduced in these three species. Within this group, *E. moerens* and *E. latro* are considered to be sister species on the basis of similarities in wing color and maculation.

Several derived character states are shared by *E. dodi* and *E. infracta*. Both have lost the sclerotized flange-like projection from the ovipositor valve, the second sub-basal diverticulum of the vesica, and both have pubescent harpes.

The phylogeny of lineage 12 has been depicted as a trichotomy but four taxa must be considered in the discussion because *E. detersa* consists of two subspecies. No characters could be found which would suggest that any two of the species are more closely related to each other than to the third. In fact, the two subspecies of *E. detersa* are more dissimilar in wing pattern than are any of the three species.

4.4.3. Evolution of the genitalia

Species of Euxoa are not well suited for studies of evolution of genitalia. Structural uniformity among species makes it difficult to determine the significance of character transformations.

Character transformations in genitalia may be arranged in three categories: those of membranous structures (bursa copulatrix, vesica), those of male valves and unci, those of ovipositor valves.

There is apparently a general correlation between transformations in the male vesica and those in the bursa copulatrix. Position (e.g. dorsal, lateral) and angle of the portion of the corpus bursae that leads to the ductus seminalis, with respect to position of the ductus bursae, is related to direction and angle of projection of the vesica. The possible importance of this, and of shape and position of accessory diverticula of the vesica, to spermatophore placement and insemination is discussed in the following section. Such transformations are probably not related directly to origin of species since many closely related species do not differ in vesica or bursa shape. The sequence of evolutionary changes in the male vesica is shown in diagram 1.

Character transformations in sclerotized structures of male genitalia are, in most instances, not lost or acquired structures but are changes in proportion. Most of these changes involve size of sacculus, length of harpe and length of sacculus extension. Although these structures are all components of the "claspers", the effects of transformations do not necessarily affect clasping ability in the sense of the "lock and key theory". It is possible that these structures have a sensory or stimulatory function during copulation. The same could be said of transformations of shape and setal arrangement of the uncus. A correlation may exist between sacculus extension length and uncus shape; species groups that have apically enlarged unci in males, have very short sacculus extensions. It is possible that in males of these groups there has been a transfer of a sensory or clasping role from sacculus extensions to unci.

Character transformations in ovipositor valves are related to oviposition habits rather than to copulation. Frequently, ovipositor valve shape or structure differs among females of closely related species (e.g. those of lineages 1, 3, 7, 8, 11 in Fig. 200). It is probable that females that differ in characters of ovipositor valve lay their eggs in different soil types; thus, there is a partitioning of resources among closely related species. The functional significance of a sclerotized projection, or stout setae, on ovipositor valves is unknown. The sequence of evolutionary changes in the ovipositor valves are shown in diagram 2.

In summary, functional and evolutionary significance of character transformations in genitalia of Euxoa species will not be known until behavioral studies have been made; this must be done with living material, not by comparison of structures using genitalic preparations.

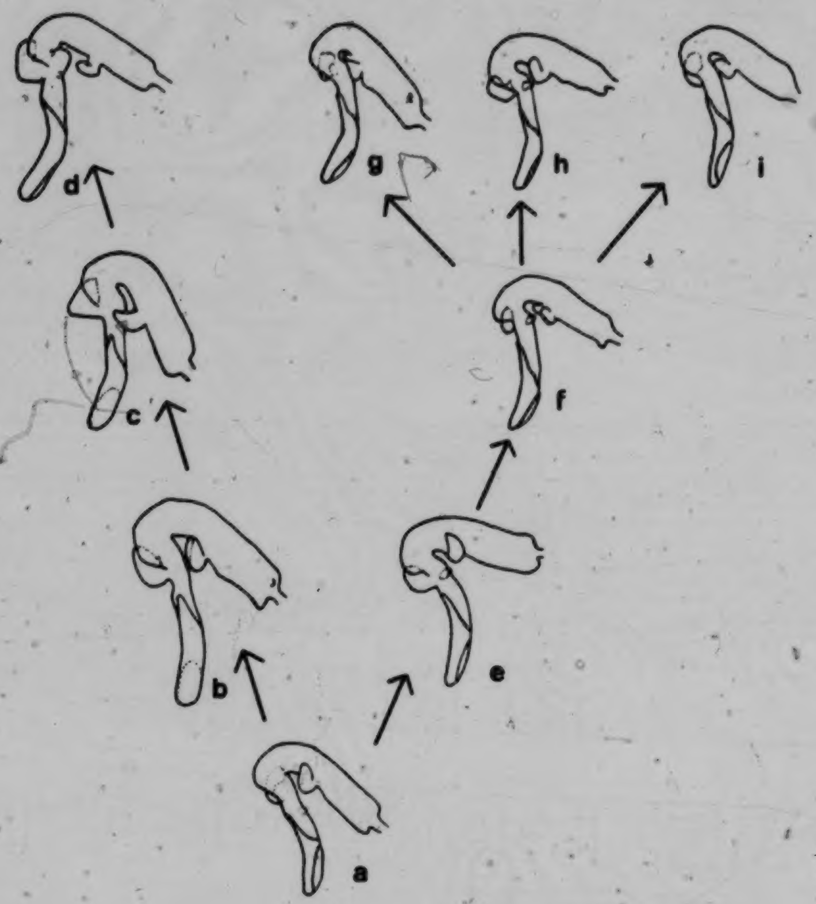


Diagram 1. Sequence of evolutionary changes of male vesica of Euxoa detersa group. a - Ancestral condition (e.g. E. agema); b - Vesica projected laterally (e.g. E. auripennis); c - Median diverticulum mesial (e.g. E. idahoensis); d - Vesica with basal twist, vesica projected dorsally (e.g. E. brevipennis); e - Extra sub-basal diverticulum present (e.g. E. teleboa); f - Median diverticulum with basal bulge (e.g. E. moerens); g - Extra sub-basal diverticulum absent (e.g. E. infracta); h - Basal bulge on median diverticulum absent (e.g. E. melura); i - Extra sub-basal diverticulum and basal bulge on median diverticulum both absent (e.g. E. detersa).

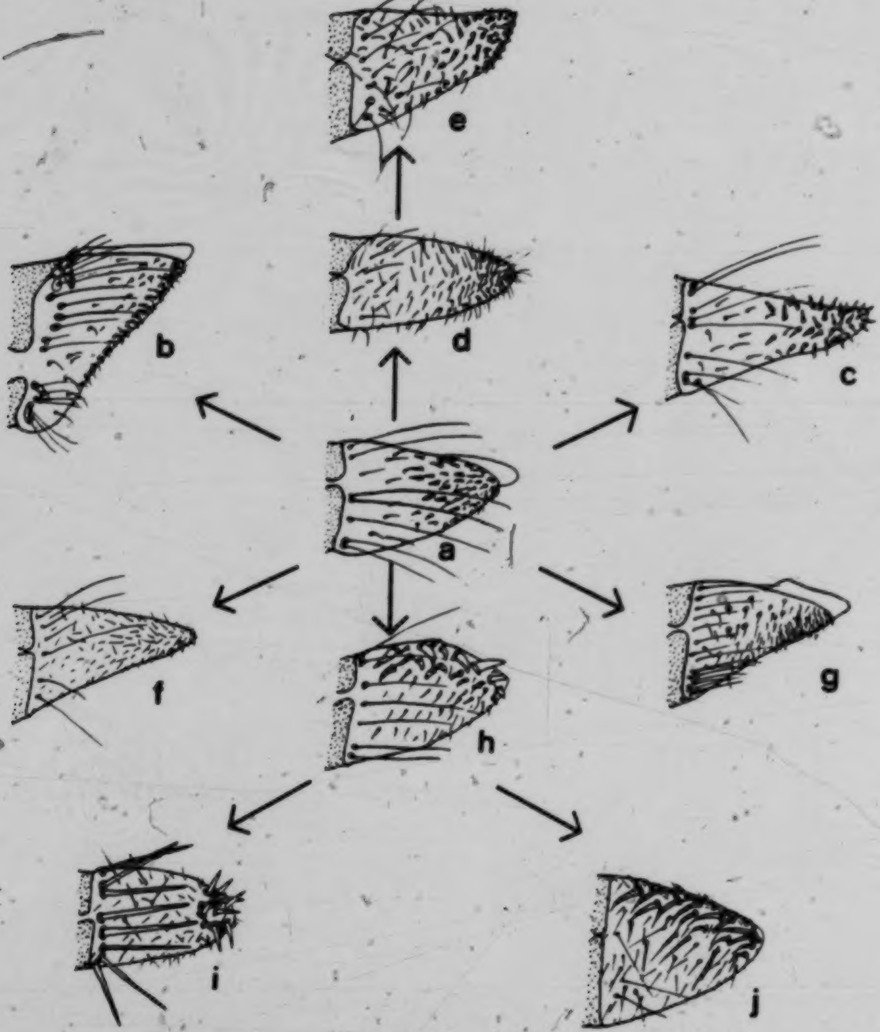


Diagram 2. Sequence of evolutionary changes of ovipositor valves of Euxoa detersa group. a - Ancestral condition (e.g. E. olivalis); b - Enlarged ventrally (e.g. E. citricolor); c - Stout setae apically (e.g. E. servita); d - Sclerotized flange absent (e.g. E. brevipennis); e - Conical setae apically (e.g. E. costata); f - Sclerotized flange absent (e.g. E. infracta); g - Sclerotized flange fin-like (e.g. E. teleboa); h - Stout setae dorsally and apically (hypothetical); i - Stout setae basally (e.g. E. dargo); j - Basal row of long setae absent (e.g. E. detersa).

4.4.3.1. The genitalia as an isolating mechanism

In any study involving evolution of male and female genitalia structures, the question arises as to whether or not the genitalia function as an isolating mechanism (the lock and key theory). This has been the subject of much debate (see review by Rentz, 1972). It is reasonable to assume that both situations exist; genitalia structure may not be an isolating mechanism among species that have elaborate behavioral or olfactory premating cues but may be an important isolating mechanism among species that lack these cues (Rentz, 1972).

Although mechanical aspects of copulation and insemination have been described for numerous species of Lepidoptera (e.g. see Arnold and Fischer, 1977; Callahan and Chapin, 1960; Ferro and Akre, 1975; Proshold _et al_., 1975; Scott, 1978; Stekol'nikov, 1965), problems in mating between members of species that have dissimilar genitalia have not been described.

In general, the spermatophore must be placed in the bursa copulatrix so that its opening is adjacent to the opening of the ductus seminalis, although successful insemination without a spermatophore has been observed (see George and Howard, 1968). While members of two species that have dissimilar male valves may be able to mate successfully (e.g. _Euxoa campestris_ (Grote) X _E. declarata_ (Walker), Byers and Hinks, 1978), those of two species in which male vesicae or female bursae are dissimilar may not be able to cross successfully. Combination of vesica shape and bursa shape is critical to positioning of the spermatophore in the bursa (Callahan and Chapin, 1960). Shape of the bursa is also important in sperm transfer since the bursa contracts and holds the spermatophore in place so that sperm is ejected into the ductus seminalis (see Proshold *et al.*, 1975).

Intergroup matings have been made in *Euxoa* (e.g. *E. campestris* (Grote) (*E. declarata* group) X *E. basalis* (Grote) (*E. basalis* group) and *E. niveilinea* (Grote) (*E. detersa* group) X *E. plagigera* (Morrison) (*E. tessellata* group), J.R. Byers, *pers. com.*), however, no fertile eggs were obtained. In each mating a spermatophore was passed to the bursa, this indicating that valve differences between the male used and a male conspecific with the female did not prevent mating; it was not determined if the spermatophore was positioned correctly in the bursa, or if sperm reached the spermatheca.

In genera in which vesica and bursa shape differ among species, the shape of these structures may be a more important isolating mechanism than is shape of male valves. Further work on the importance of spermatophore placement to insemination may prove to be very rewarding.

4.5. Conclusions

In reconstructing the phylogeny of both the species groups of *Euxoa* and the species of the *E. detersa* group, an attempt was made to rely on discrete, shared, derived character states whenever possible. Unfortunately, the paucity of suitable characters, together with susceptibility of many characters to parallel and convergent evolution, made it necessary to group taxa according to overall similarity in several instances. The Hennigian method of grouping taxa on the basis of shared, derived character states has limited applicability when dealing with morphologically similar species such as those of the *E. detersa* group. Nevertheless, the resulting phylogenies, while admittedly tenuous, do represent hypotheses with which new data can be compared and thereby provide predictive, testable models.

5. Biogeography

5.1. Introduction

In order to do a biogeographical analysis of a group, a phylogeny for the group and a knowledge of the distributions of the component taxa are required. Allopatric sister groups, or distributions with disjunctions, are particularly important for determining dispersal routes and vicariant patterns (see Platnick and Nelson, 1978; Ball, 1975; Croizat *et al*., 1974). One problem of the *E. detersa* group, for studies of this type, is that most of the species are widely sympatric. As a result, it is not possible to correlate phylogenetic data with distribution patterns and determine probable distribution and speciation patterns for the group during the glacial and interglacial periods of the Pleistocene as was done for bird taxa by Hubbard (1973) and Mengel (1964, 1970). In the *E. detersa* group, loss of resolution in possible distribution patterns for pre-Wisconsinan time makes it necessary to restrict the biogeographical analysis to late Pleistocene and Recent times.

Before attempting a biogeographical analysis of the *E. detersa* group, the major biotic provinces of western North America, and effect of Wisconsinan glaciation on them, will be reviewed as a basis for the discussion.

5.2. Geographical scope of study

In North America, ranges of most species of Euxoa are confined to relatively dry regions in the western part of the continent. This is largely due to limited temperature and moisture tolerances of the larvae. The larvae of species of Euxoa require relatively dry soil conditions so ranges of many species are limited east of the Great Plains, and in the boreal forest, by increasing rainfall (Hardwick and Lefkovitch, 1971). In addition, since larvae of most species aestivate in the soil during summer, high summer temperatures limit ranges of many species in the south. The result of these limitations is that in North America, the majority of the species in the genus are distributed in the region bounded by the deciduous forest to the east, the boreal forest to the north, and the Sonoran and Chihuahuan deserts to the south. It is this region which will be the focus of this analysis, although eastern North America will be discussed briefly since four species in the E. detersa group occur in northeastern North America.

5.3. Biogeographic regions of western North America

The biogeographic regions of western North America are determined largely by combined effects of climate and physiography. In general, coniferous forests and tundra dominate in montane regions while desert, or grassland, vegetation dominates in lowland and rainshadow areas.

The region in which the species of the *E. detersa* group live is subdivided into four major biogeographical regions, including two arid regions and two mountain systems. The two arid regions are the Great Plains and the intermontane region with the latter including the Basin and Range Province, the Colorado Plateau, and the Columbia Plateau. The two mountain systems are the Rockies extending from British Columbia and Alberta southward to New Mexico and including such outlying ranges as the Wasatch and Uinta Mountains of Utah, the Bighorn Mountains of Wyoming, and the Black Hills of South Dakota; and secondly, the Cascade-Sierra Nevada system extending from extreme southern British Columbia southward to southern California and including the Transverse Coast Ranges in southern California.

5.3.1. Vegetation

5.3.1.1. The Great Plains

The Great Plains are subdivided by most authors into three regions, defined largely on the basis of the dominant grasses (Sims et al., 1978). Tallgrass prairie, along the eastern third, is characterized by Andropogon gerardi Vitman, Sorghastrum nutans (L.) Nash, and Sporobolus asper (Michx.) Kunth; shortgrass prairie along the western third of the prairies, is dominated by Bouteloua gracilis (H.B.K.) Lag. and Buchloe dactyloides (Nutt.) Engelm. as well as Stipa comata Trin. & Rupr. and cactus (Opuntia spp.); the middle region, the mixed prairie, combines shortgrass and tallgrass species, along with Agropyron smithii Rydb. and Stipa comata (Sims et al., 1978). To the north, the prairie gives way to an aspen parkland-prairie mixture which is dominated by the grass Festuca scabrella Torr. This region has been termed fescue grassland (Coupland and Brayshaw, 1953). The regions of the northern Great Plains were classified by Coupland (1961). In this classification, shortgrass prairie and mixed prairie are combined and are characterized by the grass genera Stipa and Bouteloua.

5.3.1.2. The intermontane region

The intermontane region, as here used, is that of Fenneman (1931) and includes the Basin and Range Province, the Columbia Plateau and the Colorado Plateau.

The Basin and Range Province includes three desert regions in the south, the Mojave, the Sonoran, and the Chihuahuan deserts, all dominated by creosote bush, *Larrea divaricata* Caville (Beatley, 1975). The province also includes one desert region to the north of these, the Great Basin, which is characterized by two communities, one dominated by big sagebrush, *Artemisia tridentata* Nutt. and one dominated by shadscale, *Atriplex confertifolia* (Torr. & Frem.) Wats. The shadscale generally occupies warmer, drier sites than do the sagebrush communities. These vegetation zones have been described in detail by Billings (1949). The Mojave, Sonoran, and Chihuahuan deserts are described by many authors as hot deserts and the Great Basin as a cold desert. Floristic relationships of these deserts were studied by Rzedowski (1973). Beatley (1975) studying the transition from the creosote bush communities of the Mojave Desert to the sagebrush communities of the Great Basin reported that minimum temperature and maximum rainfall tolerances for creosote bush communities were exceeded across this transition, as were maximum temperature and minimum rainfall tolerances for the sagebrush communities.

Much of the Great Basin is between elevations of 1200 and 2000 meters (4000-6600'). Superimposed on this is a series of mountain ranges oriented in a north-south direction within the basin. A piñon-juniper woodland may exist anywhere between elevations of 1500 meters (5000') and 2400 meters (8000') with the lower limits determined by lack of moisture (Cronquist et al., 1972); however, within the basin, continuous piñon-juniper woodland is found in most sites only down to elevations of 2300 meters (7500') (Brown, 1971). Throughout much of the Great Basin the piñon-juniper association consists of singleleaf piñon pine (Pinus monophylla Torr. & Frem.) and Utah juniper (Juniperus osteosperma (Torr.) Little) (Cronquist et al., 1972). The higher ranges are forested with ponderosa pine (Pinus ponderosa Dougl.), fir (Abies spp.) and spruce (Picea spp.). The mammal communities of these disjunct conifer forests have been studied as a problem in island biogeography by Brown (1971). In the southwestern part of the Great Basin, the piñon-juniper woodland zone is slightly lower than it is farther to the north, beginning at about 2000 meters (6600') and extending to about 2900 meters (9500') (Höllermann, 1973).

The second region of the intermontane division, the Columbia Plateau, includes southeastern Washington, eastern Oregon, and southern Idaho (Sims et al., 1978) with northward extensions into southern British Columbia (Tisdale, 1947). This region has been termed palouse grassland (Tisdale, 1947; Munroe, 1956) or Pacific northwest bunchgrass (Sims et al., 1978); it is characterized by combination of xeric shrubs, especially Artemisia tridentata, with perennial bunchgrasses Agropyron spicatum (Pursh) Scribn. & Smith and Poa sandbergii Vasey (= Poa secunda of authors, see Hitchcock and Cronquist, 1974).

The third region of the intermontane division is the Colorado Plateau of eastern Utah, western Colorado, northeastern Arizona, and northwestern New Mexico. The floral communities of this region are similar to those of the Great Basin in terms of species composition but not in the relative abundance of the species. Piñon-juniper woodland is much more extensive with shadscale and sagebrush occupying arid bottomlands; the latter species is a less important constituent of the plateau flora than it is in the flora of the Great Basin. In most of the plateau area, piñon pine (Pinus edulis Engelm.) replaces the Great Basin singleleaf piñon in the piñon-juniper woodland.

5.3.1.3. The Rocky Mountain and Cascade-Sierra Nevada Mountain Systems

The vegetation of both the Rocky Mountain and the Cascade-Sierra Nevada Mountains is dominated by coniferous forests, with spruce, fir, and Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco) occupying the more mesic sites, particularly west facing slopes and higher elevations, and Douglas-fir and pines occupying the more xeric sites.

Conifer species common to both mountain systems include whitebark pine (Pinus albicaulis Engelm.), lodgepole pine (Pinus contorta Dougl.), ponderosa pine, Douglas-fir, and white fir (Abies concolor (Gord & Glend.) Lindl.). The montane forests of the Cascade-Sierra Nevada region also contain mountain hemlock (Tsuga mertensiana (Bong.) Carr.) and a variety of species of pine and fir, while those of the Rocky Mountains contain Engelmann and blue spruce (Picea engelmannii Parry and P. pungens Engelm.), limber pine (Pinus flexilis James), and subalpine fir (Abies lasiocarpa (Hook.) Nutt.).

5.4. History of the biogeographic regions of western North America

5.4.1. The late Tertiary flora

Evolution of the flora of western North America through the late Tertiary has been described by Axelrod (1976) and Tidwell et al. (1972) so only a brief review is included here. Climatic trends during this time period have been described by MacGinitie (1958), Wolfe (1978) and Matthews (1979).

The mesic deciduous hardwood-coniferous forest that covered most of western North America in the early Tertiary began to undergo changes during the Oligocene in response to a trend toward a cooler and drier climate. As this trend continued through the Miocene, many of the deciduous species in the west were eliminated from the area, and coniferous forests began to withdraw to higher elevations as an aridland flora developed in the lowlands.

The trend toward a more continental climate with increasing summer aridity, and development of open aridlands, reached a peak in late Pliocene and early Pleistocene when Sierra Nevada and Cascade Range uplift was at its maximum (Axelrod, 1976; Tidwell et al. 1972; King, 1958; Morrison, 1965). By late Pliocene time, temperature and precipitation regimes in the Great Basin were much as they are in the area today (Tidwell et al., 1972). At the start of the Pleistocene, the floral regions characteristic of the west today were well established (Tidwell, op. cit.), although mixed conifer forest was more widespread in the mountain ranges of the Great Basin (Axelrod, 1976).

The Great Plains may have supported an open woodland during interglacials with open prairie becoming widespread in the area only in Recent times (Wells, 1970b), although in a study of pre-Wisconsinan fossil pollen, Kapp (1970) suggested that the prairie habitat was present during the last (Sangamon) interglacial.

The main effect of the successive Pleistocene glacial and interglacial episodes was a sequential contraction and expansion of the aridlands coupled with expansion and contraction of the conifer woodlands.

5.4.2. Late Quaternary and Recent times

5.4.2.1. Extent of glaciation

During Wisconsinan glaciation, most of the northern half of North America was covered by one of two ice sheets. The Laurentian Ice Sheet, centered over eastern Canada, extended westward to the Rocky Mountains and southward in the west to northern Montana, southeastern South Dakota, and northern Iowa. In the east it extended southward and covered most of northeastern United States (Flint, 1957; Matthews, 1979, p.62). The Cordilleran Ice Sheet, centered over western Canada west of the continental divide, extended southward to northern Washington (Crandell, 1965) and covered most of the Rocky Mountain region south to Idaho and Montana (Richmond, 1965). South of these ice sheets, more localized Cordilleran glaciers developed in the Cascade Range of Washington and Oregon, the Wallowa and Blue Mountains of Oregon (Crandell, 1965) and in California on Mt. Shasta, Lassen Peak and along the central Sierra Nevadas (Wahrhaftig and Birman, 1965). In the Rocky Mountain region, south of the Cordilleran Ice Sheet, glaciers developed in most of the mountain ranges in Utah, Wyoming, Colorado and New Mexico (see Richmond, 1965).

Evidence for past fluctuations of alpine glaciers in western North America is difficult to correlate but in general, the last major advances of western glaciers occurred between 13,000 and 25,000 years B.P. (Porter, 1971). Final retreat of the major ice sheets began 12,000 to 14,000 years B.P. (Flint, 1957). Final disappearance of most Cordilleran glaciers occurred between 6000 and 8000 years B.P. (Porter, 1971).

5.4.2.2. Effect of Wisconsinan glaciation on flora and fauna

5.4.2.2.1. Great Plains

As mentioned in the preceding section, the northern third of the Great Plains was covered by the Laurentian Ice Sheet. In the Great Plains south of this, a more or less continuous woodland has been postulated for the region in order to explain the presence of numerous relict populations in such forested areas as the Black Hills and the Niobrara Escarpment today (Blair, 1965; Ross, 1965; Wells, 1970a; Johnson, 1975). Without further evidence, however, such conclusions can be dangerous. Hoffmann and Jones (1970) have shown that the occurrence of continuous woodland habitat in the prairies in late Pleistocene times is not sufficient to explain the presence of populations of woodland species now in the Great Plains. Presence of these species in the area may predate (e.g. see Taylor, 1965), or postdate time of occurrence of connecting woodland habitat. Lack of endemism in these areas, however, does suggest that the majority of the disjunctions are of relatively recent age.

Johnson (1975) used differentiation of disjunct butterfly populations to suggest that these populations were vicariant and not the result of recent dispersals. Ross (1965), on the other hand, used the lack of differentiation of caddisfly populations in the Black Hills as evidence of recent and frequent connections between this fauna and that of the Rocky Mountains, including continuing arrival of vagrant specimens blown into the area from montane regions to the west. It seems reasonable to assume that both situations exist, depending on mobility of the organisms concerned and rate and degree of differentiation. Former existence of continuous woodland connections across the Great Plains has resulted in presence of disjunct populations of both montane and eastern deciduous forest species in isolated woodland areas within the Great Plains (Ross, 1965; Watts and Wright, 1966; Johnson, 1975; Smith, 1957).

A more reliable indication of the presence of woodland in the Great Plains during the Wisconsinan can be drawn from the record of fossil pollen and plant macrofossils in the area. From these types of data, it is concluded that during the time of the Wisconsinan glacial maximum (20,000 - 12,000 years B.P.) the unglaciated portion of the northern Great Plains, south at least as far as eastern Kansas, supported a forest dominated by spruce with minor stands of deciduous tree species scattered through it (Wright, 1970; Grüger, 1973). Spruce was also common in the area of the Nebraska sandhills, however, it appears that the dunes were present through most of the glacial maximum and provided a xeric habitat for such dryland plants as Artemisia (Watts and Wright, 1966). The area of Nebraska sandhills has been suggested as a possible refuge area for aridland birds in the Great Plains during the glacial maximum (Hubbard, 1973). In spite of the persistence of arid habitat in the area at this time, many typical prairie plant species were apparently absent from the area making it unlikely that the sandhills supported a relict prairie flora through the Wisconsinan (Watts and Wright, 1966).

A similar picture of conifer woodland occupying presently arid and semiarid regions emerges from studies in Wyoming. Long (1971) has described a fossil assemblage from Converse County in east-central Wyoming and suggests that montane species of mammals were widespread in this presently semiarid region during the Wisconsinan glacial maximum. The area of the fossil deposits now supports a mixture of ponderosa pine woodland and sagebrush. Occurrence of ponderosa pine and western red cedar (Juniperus scopulorum Sarg.) in the now arid Laramie Basin of Wyoming in post-glacial time has been documented by Wells (1970a). Present desert vegetation was also present in the area through this time period (Wells, op. cit.).

At present, it is not possible to state how far south of central Nebraska and eastern Kansas a boreal forest type of vegetation occurred (Wright, 1971). There are indications, however, that a woodland vegetation was widespread in the southern plains during late Wisconsinan time, based on fossil pollen deposits in east-central Texas (Larson et al., 1972) and vertebrate fossil remains in northwestern Texas (Dalquest, 1965). Hafsten (1961) has studied pollen cores from the period of the full-glacial collected in the Llano Estacado region of western Texas. Both pine and spruce pollen are common in cores taken from northwestern Texas while those from southwestern Texas are dominated by pine pollen. This, however, does not represent a movement of boreal forest species southward in the plains region but represents a movement of conifer species from the mountains to the west onto the high plains during the full-glacial (Hafsten, 1961; Wright, 1971).

Generally the Great Plains region was more mesic during the late Wisconsinan than it is at present; reduced evaporation rates rather than increased precipitation may have been responsible for this. A second general trend is the frequent occurrence of fossil assemblages that include species that do not coexist today. It is believed that a more equable climate in the Great Plains during the glacial maximum allowed such a seemingly anomalous situation (Graham, 1976; Lundelius, 1967; Dalquest, 1965; Taylor, 1965).

If most of the Great Plains region was forested during Wisconsinan glaciation, then the question arises as to where the prairie flora and fauna were at this time. As mentioned above, the Nebraska sandhills may have supported some aridland species during this period but there is no evidence for the occurrence of prairie communities in the area during the Wisconsinan. The presence of endemic species of insects and mammals in the prairie region has led Ross (1970) and Hoffmann and Jones (1970) to postulate that open prairie, or at least open savannah, must have existed somewhere in the southern Great Plains or in northern Mexico during the glacial maximum. The occurrence of prairie species now disjunct in eastern Texas and northeastern Mexico does suggest that these species were distributed farther to the south in the past (Hoffmann and Jones, 1970). Prairie habitat was not widespread in northern Mexico, however, since fossil pollen deposits in the Cuatro Cienegas Basin of north-central Mexico indicate that a Chihuahuan desert flora, similar to that now present, has occupied the area since at least mid-Wisconsinan time (Meyer, 1973). Livingston (1952) has described a relict tallgrass prairie community in central Colorado which persists in localized mesic sites. This, however, only suggests that mesic-adapted plant species were probably more widespread in the past and does not indicate that open prairie occurred in the region during late glacial time.

Relative paucity of Great Plains endemics noted by numerous authors (e.g. Mengel, 1970; Munroe, 1963; Ross, 1970; Wells, 1970b) does indicate that an open prairie habitat has not been in continuous existence since the Miocene as has been suggested by some. A large proportion of the flora and fauna of the Great Plains is derived from surrounding regions and consists of the portion of those communities which are able to survive in the prairie region. In addition, however, there are species that are restricted to the Great Plains region and must have existed in xeric, relatively open areas during Wisconsinan glaciation (e.g. see Hoffmann and Jones, 1970; Mengel, 1970).

A post-glacial warming and drying trend came in the wake of the retreat of Wisconsinan glaciers and reached a peak (the altithermal) about 7200 years ago (Wright, 1971). At this time, disjunct populations of boreal mammals were probably eliminated from mountain ranges in Wyoming which now contain suitable habitat (Long, 1971) though arctic-alpine moths occur there (E.G. Munroe, pers. com.).

It has recently been suggested that development of treeless prairie in the Great Plains was due to the practice of rangeland burning by man, rather than to an inability of trees to survive in the region because of aridity (Wells, 1970b, 1970c).

During the climatic optimum, the prairie region extended farther northward and eastward than its present limit and formed the so-called prairie peninsula of the western Great Lakes region (Schmidt, 1938; Smith, 1957; Wright, 1970, 1971). With the onset of a reverse climatic trend, the prairie region retreated to its present limits leaving areas of relict prairie in Ontario and in the Great Lakes states.

In general, it can be concluded that during the last glacial maximum, most of the northern half of the Great Plains south of the ice sheet supported a forest dominated by spruce; present Great Plains endemics persisted in open pine savannah in the southern plains, in the region of the Nebraska sandhills and in other localized xeric habitats.

5.4.2.2.2. The intermontane region

The biota of the intermontane region was less affected by glaciers and continental ice sheets than by periods of increased rainfall that accompanied these times of glaciation. Although it is often difficult to correlate a pluvial with a given glacial advance, the last pluvial in the intermontane region has been shown to be equivalent to the Wisconsinan glacial maximum (Wright, 1971).

In the intermontane region, increased rainfall during the last pluvial had two major effects. First, extensive lakes were created in what are now arid basins and dry lakebeds, and second, there was a lowering of the altitudinal vegetation belts resulting in aridlands becoming more restricted and woodland becoming more widespread.

Brakenridge (1978) has argued that increased evaporation rates due to cooler annual temperatures could account for increased soil moisture and pluvial lakes without an increase in rainfall. Late Wisconsinan fossil assemblages, however, indicate a more equable climate with increased precipitation (Van Devender and Spaulding, 1979).

Although woodland was more widespread in the western deserts during the last pluvial, there has been no agreement on the magnitude or effect of the changes. Howden (1963, 1969) and Hubbard (1973) used distribution patterns and endemism to support the view that the fauna of the various desert regions, while possibly more restricted in distribution, was not displaced during the Wisconsinan. Martin and Mehringer (1965) have reviewed palynological work from the southwest for the period of the full-glacial. These authors conclude that the flora of the Sonoran Desert was confined to the vicinity of the lower Colorado River with sagebrush, piñon-juniper, and ponderosa pine communities respectively, occupying increasing altitudinal zones in what is now the Sonoran-Mojave Desert region. The basic assumption behind this conclusion is that movement of vegetation zones in response to climatic changes during the Wisconsinan was roughly zonal so that a lowering of the piñon-juniper woodland zone by 800 meters corresponded to a similar lowering of the sagebrush zone below it and the ponderosa pine zone above it. During the Wisconsinan glacial maximum, the piñon-juniper woodland zone is believed to have extended to elevations between 600 and 800 meters below those to which it extends today (Brown, 1971; Wells, 1966; Wells and Berger, 1967; Wright, 1971). Such a lowering of the piñon-juniper woodland zone would leave little, if any, room for the existence of the desert biomes as we know them today. Recent work, however, on plant debris contained in fossilized packrat middens strongly suggests that lowering of the piñon-juniper woodland zone did not lead to a corresponding lowering of the other vegetation zones. Wells (1966) studied middens from the Chihuahuan desert region and reported that although piñon-juniper woodland was widespread throughout the desert region, the desert flora was not displaced from the region but was integrated with the woodland flora. In addition, Wells found no evidence of a lowering of the ponderosa pine-fir zone in the surrounding mountains; in fact, the uneven distribution of mesophytic plant species in the mountains suggests island colonization with the mesophytic forests of these montane areas not having been connected.

A similar mixing of desert and woodland communities also occurred in the Mojave Desert, although some species of plants, such as creosote bush, were apparently absent from the area, or were restricted to the lowest most xeric sites (King, 1976; Wells and Berger, 1967).

In the Great Basin, a full-glacial climate slightly moister but no colder than it is at present was postulated by Miller (1976). Pluvial lakes occupied many of the basins at this time; Glacial Lake Bonneville, the largest of these, covered about 20,000 square miles of western Utah (Morrison, 1965). Although conifers may have grown along the edges of glacial lakes (see e.g. Cottam _et_ _al_., 1959), the region was still semiarid during the full-glacial; pollen cores from western Utah are dominated by pollen from _Chenopodium_/_Amaranthus_ for both the period of the full-glacial and for Recent times (Tidwell _et_ _al_., 1972).

Unfortunately, for most of the Great Basin region, plant remains dating from glacial times are lacking and effects of the last pluvial on the biota must be discerned from present day distribution patterns. Mosquin (1964) used chromosomal and distributional data from a study of _Clarkia_ _rhomboidea_ to suggest that ponderosa pine and fir forests were widespread in the Great Basin during the Wisconsinan glacial maximum. _Clarkia_ _rhomboidea_ is presently distributed in the mountains surrounding the Great Basin in ponderosa pine and fir forests, but occurs within the Basin only near Winnemucca, Nevada. There are two problems with the conclusion that

C. rhomboidea was distributed throughout the Great Basin during the last glacial. First, it would be expected that this species would occur on other mountains in the Great Basin that support suitable habitat; second, it would be difficult to explain why crosses between plants from Winnemucca and those from Sierra Nevada colonies are more fertile than are crosses between plants from Winnemucca and those from northern Utah.

Brown (1971, 1978) studied the mammalian fauna of the mountain ranges within the Great Basin as a problem in island biogeography and has come to a conclusion considerably different from that of Mosquin. Diversity of the mammalian fauna associated with piñon-juniper woodland varies from range to range. Number of species on each range is correlated with amount of available habitat and not with distance, either between ranges, or between a range and either the Rocky Mountain region or the Sierra Nevada region. This suggests that these montane faunas are relicts from a period when woodland was more widespread and are not products of continuing colonization and extinction. In addition, of the species of mammals associated with ponderosa pine and fir forests on the mountains surrounding the Great Basin, none occurs on any of the mountain ranges within the Basin, although suitable habitat is present (Brown, op. cit.). The avifauna associated with ponderosa pine and fir forests, on the other hand, is well represented on the ranges within the Basin, wherever suitable habitat occurs. From these data, Brown (op. cit.) concluded that during the full-glacial, piñon-juniper woodland was widespread in the Great Basin while ponderosa pine and fir forests remained restricted to montane areas.

The late-glacial vegetation of the Columbia Plateau was originally described as lodgepole pine parkland by Heusser (1965); however, a recent reexamination of the situation by Mack (1976) led to a radically different interpretation of the data. The pine pollen has been reidentified as being that of *Pinus albicaulis* or *P. monticola*. In addition, pollen from spruce and fir is also present suggesting that the area supported a subalpine vegetation during full-glacial rather than pine parkland. Presence of areas of patterned ground supports the view that treeless, alpine-like areas were present as well (Mack, 1976).

At present, little information is available about full-glacial vegetational changes on the Colorado Plateau but it is probable that these were similar to those in the Great Basin.

Evidence for a post-glacial maximum in temperature and aridity in the intermontane region has been presented by a number of workers. Martin (1963) found no palynological evidence for an altithermal interval in the arid southwest, but apparently, there is geological evidence for it (Wright, 1971). Hybrid swarms between *Pinus edulis* and *P. monophylla* (see Lanner and Hutchison, 1972) and between *Quercus turbinella* and *Q. gambelii* (see Cottam *et al.*, 1959) at localities in northern Utah outside of the present distribution of one, or both, parental species have been used as evidence of a post-glacial altithermal period when *Quercus turbinella* and *Pinus edulis* were distributed farther to the north than they are at present.

In general, data from the intermontane region suggests that during the Wisconsinan glacial maximum subalpine and alpine vegetation grew in the area of the Columbia Plateau; piñon-juniper woodland was widespread through most of the Great Basin and southwestern desert regions. Aridland vegetation was not displaced from these regions but persisted in association with piñon-juniper woodland. Although ponderosa pine and fir forests probably dominated the vegetation of plateau and montane areas, mesic forests were not widespread in lowland areas during the glacial maximum.

5.4.2.2.3. The Rocky Mountain and Cascade-Sierra Nevada Mountain systems

The effect of climatic changes during the Wisconsinan in western North America was that montane vegetation was forced to lower elevations.

In the Rocky Mountain region, pine, spruce, and fir forests apparently occupied areas between 600 and 800 meters below those occupied at present (Baker, 1970; Maher, 1963; Wright, 1971). Areas in southwestern Idaho where sagebrush presently grows were forested with spruce and pine during the glacial maximum (Wright, 1971). Similarly, lowland areas in northwestern Wyoming formerly supported subalpine or alpine vegetation (Baker, 1970). Movement of forest vegetation into lowland areas during the last glacial maximum eliminated aridland connections between the Great Basin and the Great Plains and isolated the flora and fauna of these two regions (e.g. see Hoffmann and Jones, 1970).

Full-glacial deposits of pollen in the Sierra Nevada region have not been studied; however, some conclusions can be drawn from a study made by Adam (1967) on late-glacial and Recent deposits in central Sierra Nevada. Changes in vegetation zones of the Sierra Nevada from late-glacial to Recent times were less dramatic than were those that occurred in the Rocky Mountain region. An area near Lake Tahoe, which presently supports a mixed conifer forest, supported a vegetation during Wisconsinan time similar to that of the zone of stunted sagebrush that presently occurs in the region above treeline (Adam, 1967). Fossil pollen, and soil profiles, from coastal California indicate that a Mediterranean climate was maintained in the area throughout the late Quaternary (Johnson, 1977).

5.4.2.2.4. Speciation during Wisconsinan and Post-glacial times

There has been much debate in the literature as to whether or not speciation occurred as a result of distributional changes caused by Wisconsinan glaciation. Coope (1970) has demonstrated with fossil material that a number of beetle species formerly thought to have arisen during Wisconsinan time are actually much older. From these findings, Coope has concluded that little, if any, speciation has occurred in insects in the latter half of the Quaternary. In view of different evolutionary rates of various insect groups, and the extremely rapid speciation ability known for some groups such as the acalyptrate Diptera (Bush, 1973, 1975), such an extrapolation seems simplistic. Briggs (1966) has discussed some factors that may lead to rapid speciation in disjunct populations. For these reasons, the possibility of speciation in the *E. detersa* group resulting from distributional disjunctions during the late Quaternary has been maintained as a working hypothesis.

5.5. Faunal regions

Present distribution of an organism is the product of numerous factors. Distribution of a species may be limited by such factors as available habitat, dispersal ability, climate, and interspecific competition. Superimposed on these factors, are effects of successive Quaternary glacial and interglacial episodes, which occurred during the Quaternary, on the biogeographic regions of North America.

It has long been recognized that similar distribution patterns are shared by many species. This similarity may be due to past events in earth history, such as effect of continental drift on intercontinental distribution patterns. On a regional basis, however, distributional similarities are more frequently related to environmental factors.

Van Dyke (1919, 1940) and Linsley (1958) have described and categorized the distribution patterns most frequently encountered in species of Coleoptera in western North America. Similar distribution patterns are not only shared by beetle species but also by many species of plants and animals. Initially, Van Dyke (1919) divided western United States into six faunal regions: Vancouveran, Sierran, Californian, Great Basin, Sonoran, and Canadian. Later, Van Dyke (1940) reduced the number of faunal regions and expanded the size of the remaining ones. The Vancouveran faunal region included the coniferous forest regions of the western mountains and the Pacific coast; the Canadian faunal region included the southern portion of the boreal forest and the northern prairie regions; the Sonoran faunal region included the Great Basin, the southwestern deserts, and the most arid portions of the western Great Plains; the remainder of the Great Plains was included with eastern United States in the Alleghenian faunal region. In a discussion of distribution patterns of species of Cerambycidae in western North America, Linsley (1958) adopted the faunal regions of Van Dyke but subdivided them.

Munroe (1956), in a review of the insect fauna of Canada, divided distribution patterns into ten generalized patterns, many of which were further subdivided. Of these ten, two, namely, the Central and Western Ranges, are particularly relevant to this discussion. Munroe subdivided the Central Ranges into two components: Great Basin-Columbia Plateau distributions, and Great Plains distributions. The Western Ranges were subdivided into coastal and montane distribution patterns. The Central and Western Ranges of Munroe (1956) are roughly equivalent to the Sonoran and Vancouveran faunal regions respectively of Van Dyke (1940).

While it is convenient to discuss distribution patterns in terms of generalized patterns and faunal regions, it must be kept in mind that these are groupings of convenience. The distribution of each species is determined by interaction of many factors; no two species would be expected to be affected by this matrix of factors in exactly the same way. As a result, two species which have similar distribution patterns under present conditions may not have had similar distributions in the past under different environmental conditions. A change in one environmental factor may affect one species and not another. Formerly, biogeographers found it necessary to search for refugia for faunal units such as the "Great Basin fauna" or the "Sonoran fauna". Under changing environmental conditions, however, communities would not be expected to move as units, but rather, each species would react independently to the changes (e.g. see Whittaker, 1967). As mentioned previously, a more equable climate in the Great Plains during Wisconsinan glaciation is thought to have allowed species of mammals which are now allopatric to occur sympatrically (Dalquest, 1965; Graham, 1976). A comparable situation was described for the flora of the southwestern deserts by Wells (1966) and Wells and Berger (1967).

In conclusion, while it is convenient to group species with similar distribution patterns to facilitate discussion, it cannot be assumed *ipso facto*, that these species had similar distributions in the past.

5.6. Biogeography of the Euxoa detersa group

In general, ranges of most species in the E. detersa group are in either the Vancouveran faunal region (Van Dyke, 1940; Western Ranges (Munroe, 1956)), or the Sonoran faunal region (Van Dyke; Central Ranges (Munroe)). The division is essentially between species associated with forested areas and those associated with open aridlands. The habitats in which each species of the E. detersa group is found are shown in table 4.

For this discussion, the species have been arranged in two broad groups: aridland species, and forest species. Species from both of these habitat groups, however, occur together in some intermediate habitats, particularly piñon-juniper woodland and open pine parkland. Both present and past distributions are considered.

The ancestral stock of the E. detersa group was probably adapted to open aridlands with forest dwelling the derived condition. This assumption is based on three things: first, the majority of species in Euxoa occur in open aridlands; second, most species in the sister group of E. detersa group (see figure 199) occur in open aridlands; third, the assumption that the ancestral stock of the E. detersa group occurred in aridlands is more parsimonious since it involves 7 invasions into woodland habitats; the reverse direction of movement would require 10 invasions of aridland habitats (see figure 200). A reversal in the general pattern of invasion of woodland habitats from aridland habitats has occurred in E. clausa, and possibly in E. moerens (see figure 200).

Table 4. Habitat preference for species of the *Euxoa detersa* group

Species	Habitat				
	Larrea, Sagebrush	Grassland	Piñon-juniper woodland	Pine parkland	Conifer forests, aspen
costata				•	●
castanea				●	●
foeminalis				●	
idahoensis			•	●	●
clausa	?	?			
brevipennis	●		•		
servita				●	●
redimicula				•	●
auripennis				•	●
arizonensis			•	●	•
olivalis		•	●	•	
agema				●	●
oblongistigma	●	●	•		
citricolor	●		•		
tronella	●	•	•		
teleboa		●	●		
moerens	•	●	●	•	
latro				●	●
murdocki			•	●	•
dodi		●	•	•	
infracta			•	●	•
laetificans			•	●	•
quadridentata	•	●	●	•	•
inscripta	●	•	•		
unica		?			?
niveilinea	•	●	•	•	
dargo	•	●			
melura	?		?		
detersa		●			
cicatricosa	●	●	•	•	
recula	●		•		

● - common
• - uncommon
? - data insufficient

5.6.1. Present distributions

Distribution maps for the species in the E. detersa group are shown in figures 158 to 185. For a biogeographic analysis, it is necessary to know where a species does not occur, as well as where it does. For this information, two factors are considered: first, distribution of suitable habitat (see figure 187), and second, presence or absence of a species at a locality where seemingly suitable habitat exists where a collection was made at the right time of the year. It is, of course, very difficult to show that a species does not occur in an area. At each of the localities sampled during the Euxoa survey (see figure 186), habitat notes and photographs were taken. If a species is frequently collected in a given habitat in one region, and not collected in comparable habitat in a second region, it is assumed that the species does not occur in the latter region. While such conclusions may generally be true, they must be used with caution. Euxoa latro, for example, was thought to be restricted in distribution to the Cascade-Sierra Nevada region (see figure 173). This assumption was further supported by apparent absence of the species in suitable habitat in the Rocky Mountain region and in mountains of the intermontane region. This conclusion, however, was shown to be erroneous by the recent discovery of E. latro in the La Sal Mountains of Utah.

5.6.1.1. Aridland species

Included in this group are species found most commonly in open grassland and sagebrush habitats. These species are also found in piñon-juniper woodland or open pine parkland where aridland vegetation is widespread. Only rarely are they collected in forested areas. Most aridland species are distributed in both the intermontane region and in the Great Plains, although many are more widely distributed in one region than the other. Species which are distributed in both regions are: *E. brevipennis*, *E. oblongistigma*, *E. citricolor*, *E. tronella*, *E. dodi*, *E. inscripta*, *E. dargo*, *E. melura*, and *E. cicatricosa*. *Euxoa recula* is restricted to the intermontane region; *E. clausa*, *E. niveilinea*, and *E. detersa personata* are largely restricted to the Great Plains, although the latter two are found as far east as the Great Lakes region.

Ranges of species that occur in both the intermontane region and the Great Plains are connected in relatively low, arid corridors that extend through the Rocky Mountain region in northeastern Utah and southwestern Wyoming, and in eastern Idaho and southwestern Montana (see figure 187). In addition to these two corridors, a third connection between intermontane and Great Plains distributions is in New Mexico south of the Rocky Mountains. Four species (*E. brevipennis*, *E. citricolor*, *E. quadridentata*, *E. cicatricosa*) are distributed through this latter connection, all four also occur in the more northerly corridors.

One aridland taxon, *Euxoa d. detersa*, is distributed in eastern North America along the Atlantic seaboard in beach and dune areas.

Four species might better be considered as intermediate between aridland species and forest species in habitat preference. Of these, three species (E. olivalis, E. teleboa, E. moerens) occur in open prairie habitat in the Great Plains, but in the intermontane region they are in piñon-juniper woodland, and avoid open sagebrush areas. They are included in this section, with aridland species, because they are widely distributed in the Great Plains and intermontane regions and largely avoid the conifer forests of the montane areas. The fourth species (E. quadridentata), is restricted to arid and semiarid habitats in most of its range but along the Cascade-Sierra Nevada axis, it is found in pine and fir forests.

5.6.1.2. Forest species

The species in this group are usually distributed in forested areas characterized by species of pine, fir, spruce, and aspen. The thirteen forest inhabiting species are arranged in two groups, first, those which also live in xeric piñon-juniper woodland (*E. idahoensis*, *E. arizonensis*, *E. murdocki*, *E. infracta*, *E. laetificans*), and second, those which do not occur in the more xeric woodlands (*E. costata*, *E. castanea*, *E. foeminalis*, *E. servita*, *E. redimicula*, *E. auripennis*, *E. agema*, *E. latro*). Species in the first group occur in the Great Basin wherever suitable habitat exists. Species in the second group occur in the mountain ranges surrounding the Great Basin, but rarely occur within the Basin, even in montane areas that support suitable habitat. Most of the species that are distributed in the Rocky Mountain region, and *Euxoa redimicula* which is distributed in eastern North America, also occur in wooded areas in the Great Plains.

5.6.2. Past distributions

Although habitat preferences for species in the E. detersa group may not have been identical in the past with those of the species today, it is assumed that they were at least similar.

5.6.2.1. Aridland species

Most of the taxa included in this group are distributed in western North America; however, the eastern subspecies of Euxoa detersa occurs in xeric habitats in the east. Euxoa d. detersa is distributed in beach and dune areas along the Atlantic coast from South Carolina northward to the Gaspé Peninsula and the St. Lawrence River region. This species may have lived during the Wisconsinan either on the then emergent Sable Island Banks off Nova Scotia (see Howden et al., 1970) or along the Atlantic seaboard in southern United States. Very arid conditions prevailed in southeastern United States during the glacial maximum (Watts, 1971; Whitehead, 1967) with active sand dunes present in the Carolinas (Whitehead, 1973).

In western North America, most aridland species live in both open areas and in piñon-juniper woodland; therefore, they may have occurred in either, or both, of these habitats during the Wisconsinan. Most of the Great Plains region was unsuitable for aridland species during the last glacial maximum because of the presence of the Laurentian ice sheet in the north and conifer forests south of this. There are, however, areas within the Great Plains region which may have provided suitable habitat for aridland species during

Wisconsinan time including localized xeric habitats along water courses and on south facing slopes.

Euxoa detersa personata lives in dune areas and was probably distributed in the Nebraska sandhills during the Wisconsinan. *Euxoa niveilinea*, which is common in the sandhills today, may also have occurred in the area at that time.

The remaining aridland species in the *E. detersa* group that are distributed in the Great Plains are not in dune habitats. Although these species occur in treeless habitats in the Great Plains, they also occur in piñon-juniper woodland to the west of the Plains; this habitat was present during the Wisconsinan glacial maximum in the Chihuahuan desert area (Wells, 1966) and probably in basin areas in Wyoming (Wells, 1970a). Most of these species, however, are more widely distributed in the intermontane region and their occurrence in the Great Plains may be of post-glacial origin.

A prairie-like habitat is believed to have existed in southeastern Texas during the Wisconsinan; disjunct populations of prairie species occur in the area today (Hoffmann and Jones, 1970; Hubbard, 1974). Several species of *Euxoa*, including *E. niveilinea*, fit this type of pattern in that disjunct populations occur in eastern Texas today.

Aridland species which presently occur in the intermontane region could have existed in the area, in piñon-juniper woodland, during Wisconsinan time. Extent of suitable habitat, however, was greatly reduced by expansion of conifer woodlands in montane areas, and by presence of pluvial lakes in basin areas. Also, most of the

Columbia Plateau was unsuitable for aridland species during Wisconsinan time because of subalpine conditions in the area (Mack, 1976).

Within the intermontane region, *Euxoa dargo* is restricted to the palouse grassland of the Columbia Plateau. Presumably, maximum temperature, or minimum moisture, tolerances of *E. dargo* are exceeded in the Great Basin, or *E. dargo* is unable to compete successfully with other Great Basin species. If *E. dargo* was distributed in the Great Basin during Wisconsinan time, relict populations did not persist in the area. This species may have been distributed in the Wyoming Basin or in the southwestern Great Plains during Wisconsinan time, and its occurrence in the intermontane region of post-glacial origin.

Without a fossil record, one cannot determine the past distribution of a species of *Euxoa* with any degree of certainty. Some general inferences, however, may be made. Ranges of aridland species were reduced during Wisconsinan time. In the Great Plains, most aridland species were probably restricted to small pockets of suitable habitat as well as to piñon-juniper woodland in the Wyoming Basin and in the area of the southwestern plains and Chihuahuan Desert. At least two species probably lived in the Nebraska sandhills and one species in southeastern Texas. In the intermontane region, aridland species lived in areas of piñon-juniper woodland in most of the region except the northern portion. Aridland connections between the Great Plains and the intermontane region were eliminated during the glacial maximum.

5.6.2.2. Forest distributions

During Wisconsinan time, conifer forests were widespread in the Great Plains region south of the ice sheet. Seven species usually associated with forested areas are presently widely distributed in the Rocky Mountain region (*E. castanea*, *E. servita*, *E. auripennis*, *E. agema*, *E. idahoensis*, *E. infracta*, *E. laetificans*). Most of these species were probably widely distributed in the Great Plains region during the glacial maximum since only one (*E. agema*) does not occur in disjunct forested areas within the Great Plains today. One species (*E. redimicula*) now living in coniferous wooded areas and deciduous gallery forests within the Great Plains, was probably widely distributed in the area in the past; it is now mostly confined in distribution to eastern North America.

In the intermontane region, piñon-juniper woodland was widespread during the Wisconsinan but more mesic conifer forests in montane areas remained disjunct (see Brown, 1971). Species which can tolerate semiarid conditions and occur in piñon-juniper woodland (see 5.6.1.2.) were widely distributed in the intermontane region during the Wisconsinan; species which are restricted to more mesic conifer forests were distributed in the mountain ranges around the intermontane region, and were, for the most part, prevented from reaching suitable habitat on mountain ranges in the intermontane region by the intervening unsuitable habitat. There are a few exceptions to this; however, the general absence of forest-loving species in suitable habitat in the intermontane region attests to the rarity of species being able to disperse across the arid lowlands.

5.6.3. Development of present day distribution patterns

Ranges of species in the E. detersa group changed radically following retreat of Wisconsinan ice sheets.

Aridland species in the southern and western Great Plains were able to expand their ranges to the north as prairie habitat became available. A pine savannah may have existed in the Great Plains at this time with the treeless, prairie condition becoming predominent only after elimination of trees by prairie fires (Wells, 1970b, 1970c). Ranges of Euxoa niveilinea and E. detersa personata expanded eastward into the western Great Lakes region during the post-glacial climatic optimum when the prairie peninsula was forming. Further eastward expansion of the range of E. detersa personata took place by way of beach habitats. Ranges of E. detersa personata and E. d. detersa presently overlap in the lower St. Lawrence Valley. Populations of E. detersa from the region of overlap appear to be both intermediate and more variable than do those from the parental zones; these are characteristics of hybrid zones in general (see Schueler and Rising, 1976).

With expansion of prairie in the Great Plains came withdrawal of forests from the area. Species in the E. detersa group that require forest habitats persist in the Great Plains region only in wooded sites on scarps and in river bottoms.

Similar, though less dramatic, changes took place in the intermontane region. As piñon-juniper woodland moved to higher elevations and pluvial lakes dried, species that were able to exist in open aridlands became more widespread while those that require woodland conditions became more restricted in distribution.

Higher summer temperatures and increasing aridity in the Rocky Mountain region led to development of arid corridors that connected aridlands of the intermontane region with those of the Great Plains region. Since aridlands were eliminated from most of the Great Plains during Wisconsinan time while those of the intermontane region remained widespread, it is probable that more Great Basin aridland species invaded the Great Plains than the converse. Eight species of mammals distributed in sagebrush communities in the Great Basin and the northern Great Plains, are believed to have invaded the Great Plains in post-glacial time (Hoffmann and Jones, 1970). Seven species in the E. detersa group (E. brevipennis, E. oblongistigma, E. citricolor, E. tronella, E. moerens, E. inscripta, E. melura) are widely distributed in the intermontane region but occur only in arid areas in the northern Great Plains; most of these species probably entered the Great Plains region in post-glacial time.

In the intermontane region, Euxoa inscripta occurs in the lower elevations of the central Sierra Nevada and in the Colorado Plateau area; it apparently does not occur in similar habitat within the Great Basin. The reason for this apparent disjunction is not clear but it is possible that post-glacial extremes in temperature and aridity eliminated the species from the intervening area.

Two species (E. dodi, E. dargo) are more widely distributed in the Great Plains than they are in the intermontane region. Present ranges of these two species are almost completely within territory that was unsuitable for them during Wisconsinan time. They do, however, occur in the southwestern Great Plains and may have occurred there during the Wisconsinan as well.

In late-glacial and post-glacial times two major changes occurred in distributions of forest inhabiting species of the western mountains. First, as Wisconsinan ice sheets retreated, these species spread northward as suitable habitat became available. Euxoa costata and E. castanea, which were allopatric during the full-glacial, became sympatric in southern British Columbia (Fig. 188). Second, populations of species in the isolated ranges of the central and southern Rocky Mountain system became disjunct in post-glacial time as aridlands developed in the intermontane lowlands. Disjunctions in ranges of two species in the E. detersa group (E. agema Fig. 191, E. latro Fig. 193), however, cannot be explained in this way. The population of Euxoa agema in the Ruby Mountains of Nevada could have reached the area in three ways: by dispersal across arid lowlands; through former connections of suitable habitat in lowlands; or, by the species formerly being able to exist in habitats more arid than those which it inhabits today. There is little evidence for existence of mesic forest connections between the Ruby Mountains and the Rocky Mountains during Wisconsinan time. Expansion of conifer forests at this time, however, would have made dispersal more probable since size and severity of the aridland barrier was reduced. Occurrence of Euxoa latro in the La Sal Mountains of Utah (see figures 173 and 191) may be the result of long distance dispersal or vicariance. No other species was found with a distribution pattern similar to that of E. latro, although some species of plants are distributed in Utah only in the La Sal Mountains (see Welsh _et_ _al_., 1975). It is possible that with more intensive collecting in the Colorado Rockies, _E_. _latro_ will be found in that area.

5.6.4. Speciation in the late Quaternary

In many groups that contain species that do not disperse well, it is possible to correlate ranges of some constituent taxa with past events in earth history (see Rosen, 1978). Present distributions of closely related, largely allopatric species are frequently interpreted as results of speciation during Quaternary time (e.g. see Hubbard, 1973; Mengel, 1964, 1970; Ross, 1965). In order to examine the possibility of using distribution patterns to study speciation in the *E. detersa* group, maps were prepared to compare ranges of sister species (figures 188-198).

Evidence for speciation during Wisconsinan time in terms of distribution patterns, may be lacking for one of three reasons: speciation may have occurred earlier than was suspected; sympatric speciation may have occurred; one, or both, of the sister species may have colonized the territory of the other producing widely sympatric sister species.

Although there is no evidence to suggest that sympatric speciation has occurred in the *E. detersa* group, evidence from other taxa suggests that it may occur in some species groups. In some species, ecotypic forms appear to intergrade little at some localities where they occur together, but intergrade extensively at other localities. Although it is possible that these forms arose allopatrically, a shift to a radically different soil type could be selected for in much the same way as has been postulated for host plant shifts by Bush (1973, 1975).

In each of two species pairs of the *E. detersa* group (*E. citricolor*-*E. tronella* (Fig. 192), *E. laetificans*-*E. quadridentata* (Fig. 195), the sister species are widely sympatric, thus giving little indication of where or when speciation occurred. Speciation in the *E. laetificans*-*E. quadridentata* lineage probably took place in pre-Wisconsinan time since subspeciation in *E. quadridentata* (see below) appears to have occurred during or before Wisconsinan time.

Four species pairs (*E. infracta*-*E. dodi* (Fig. 194), *E. q. quadridentata*-*E. q. flutea* (Fig. 195), *E. inscripta*-*E. unica* (Fig. 196), *E. melura*-*E. dargo* (Fig. 197) have ranges that suggest differentiation of the sister taxa in separate Great Basin and Great Plains centers, possibly as recently as during Wisconsinan time. Differentiation between *E. infracta* and *E. dodi* could have occurred either with *E. infracta* distributed in the intermontane region and invading the prairie region in early post-glacial time when the Great Plains were still forested, or with *E. infracta* distributed in both the intermontane and prairie region. In either situation, *E. dodi* was probably isolated in semiarid areas of the southwestern Great Plains region. It may be premature to consider *E. inscripta* and *E. unica* as Great Basin-Great Plains sister species, especially considering that *E. unica* is known from only two specimens, these from formerly glaciated south-central Saskatchewan. A comparable situation, however, was described by Munroe (1961, 1975) in which *Frechinia laetalis* (Barnes and McDunnough) occurs in the Great Basin and its sister species, *F. criddlealis* (Munroe), is known from specimens collected in southwestern Manitoba.

Examples of differentiation of taxa in Great Basin and Great Plains centers do not appear to be common. Hubbard (1973), in reviewing avian evolution in North American aridlands, found only one species pair which may have differentiated in Great Basin and Great Plains refugia; Hoffmann and Jones (1970) found only three examples of this in the mammals.

Two species pairs (*E. agema-E. oblongistigma* (Fig. 191), *E. latro-E. moerens* (Fig. 193)) have ranges in which one species occurs in the aridlands of the Great Basin and the northern Great Plains, and the second species occurs in conifer forests in the mountains surrounding the Great Basin. These ranges give little indication of when these lineages speciated. The sister species of each of these species pairs (*E. olivalis* and *E. murdocki* respectively) are of no help since they are sympatric with both species in their sister group and are in the habitats of both as well.

One species pair (*E. costata-E. castanea* (Fig. 188)) has a montane distribution in which *E. costata* is distributed in the Sierra Nevada and Cascade Ranges and *E. castanea* is distributed in the Rocky Mountains. Although the two species were isolated during Wisconsinan time, it is possible that their origin as species occurred at an earlier time. Ross (1965) gives three examples of species pairs in which the component species have ranges similar to those of *E. costata* and *E. castanea*.

In three instances, ranges of three species are illustrated in the figures. These are *E. foeminalis-E. idahoensis-E. clausa* (Fig. 189), *E. redimicula-E. auripennis-E. arizonensis* (Fig. 190), and *E. detersa*-*E. cicatricosa*-*E. recula* (Fig. 198).

The ranges of *E. recula*, *E. cicatricosa* and *E. detersa personata* suggest that these species may have been isolated in the Californian, Great Basin (or Sonoran), and Nebraskan Refugia respectively, of Hubbard (1973); *E. d. detersa* was distributed in arid habitats along the Atlantic seaboard. Once again, however, it is not possible to determine if these taxa differentiated during Wisconsinan, or in pre-Wisconsinan time.

In the *E. redimicula*, *E. auripennis*, *E. arizonensis* series, specimens of the latter two species are more similar to each other, both structurally and in maculation, than they are to those of *E. redimicula* (see Lafontaine, 1974a). *Euxoa arizonensis* could have differentiated during Wisconsinan time as a southern isolate of an *E. auripennis*-like ancestor. As stated in section 4, a pre-Wisconsinan origin for *E. redimicula* is postulated, since both *E. auripennis* and *E. redimicula* occur in disjunct woodland areas within the Great Plains and the two may have been widely sympatric in the Great Plains region during Wisconsinan time when it was forested. It is possible, however, that the range of one, or both, of these species was extended into the Great Plains region in postglacial time.

The situation of the *E. idahoensis*, *E. foeminalis*, *E. clausa* series is similar to that described above, in that *E. foeminalis* may have differentiated from an isolated population of an *E. idahoensis*-like ancestor during Wisconsinan time. Also, specimens of *E. idahoensis* and *E. foeminalis* are more similar to each other, in maculation and habitus, than they are to those of E. clausa. The degree of differentiation, however, may not necessarily reflect the age of the taxon.

In conclusion, ranges of many sister species pairs in the E. detersa group are what would be expected from allopatric speciation during the Wisconsinan. In each situation, however, it can be argued that the species were already present before the Wisconsinan and that the ranges reflect allopatric isolation during the Wisconsinan and not speciation.

5.7. Summary and concluding remarks

Most of the species in the E. detersa group are distributed either in open aridlands, or in forested areas.

The aridland species are usually associated with grassland and sagebrush areas, and more rarely, with areas in the southwest that are dominated by creosote bush. Most aridland species also occur in xeric piñon-juniper woodland.

Forest species are those usually associated with areas where species of pine, spruce, fir, and aspen abound, and where the soil is well-drained. They do not live in conifer forests where the soil is wet, or boggy. Five of the 14 forest species also occur in piñon-juniper woodland. Generally, forest species are distributed in the forested regions of southern and western Canada and in conifer forests in the mountain ranges of western North America. Most species that are distributed in the Rocky Mountain region are also in woodland areas in the Great Plains. Species that occur in piñon-juniper woodland are widely distributed in the Great Basin, wherever suitable habitat exists. Species that are distributed in ponderosa pine and fir forests, but not in piñon-juniper woodland, are rarely found in the Great Basin region, even in areas where suitable habitat is present.

In the absence of a fossil record, evidence for past distributions of species in the E. detersa group must be based on present day distributions and on the past distribution of the habitats in which they occur. Distributional disjunctions, especially those found in a number of species, may be indicative of former distribution patterns. Evidence for the past distribution of habitats is based largely on fossil pollen deposits and on plant macrofossils.

From these data, it is concluded that expansion of conifer forests during the Wisconsinan glacial maximum greatly reduced the amount of open aridland habitat in western North America. In the Great Plains, most aridland species were probably distributed in piñon-juniper woodland in the Wyoming Basin, the southwestern Great Plains area, and the Chihuahuan Desert. Some species were probably distributed in aridlands in the Nebraska sandhills, southeastern Texas, and local areas of suitable habitat within the Great Plains region. In the intermontane region, during the Wisconsinan, aridland species were distributed in piñon-juniper woodland in the Great Basin and Mojave Desert. Aridland connections between the intermontane region and the Great Plains were eliminated during the glacial maximum.

Forest species were widespread in the Great Plains south of the Laurentian Ice Sheet during Wisconsinan time. In the intermontane region, species that occur in piñon-juniper woodland were widespread in the region during the glacial maximum. Species restricted to more mesic pine and fir forests were, for the most part, prevented from reaching suitable habitat in mountain ranges in the Great Basin by unsuitable habitat in the intervening lowlands.

Present ranges of many sister species are what would expected if two populations of their common ancestor had been isolated during Wisconsinan time and had differentiated. These types of distribution patterns are frequently interpreted as resulting from isolation and speciation during Wisconsinan time. These distribution patterns, however, provide no evidence about age of the constituent taxa. While distribution patterns may suggest that sister species were isolated in different refugia during Wisconsinan time, they provide no evidence to demonstrate that these taxa speciated during this period of isolation.

If a biogeographical hypothesis is to be of value to other biogeographers, it must be falsifiable and have predictive value (Ball, 1975).

One method of falsifying biogeographical conclusions is to falsify the phylogeny upon which those conclusions are based. Different techniques, such as use of serological data, or discovery of previously overlooked characters, may cast doubt on sister group relationships used in the biogeographical analysis. Also, the discovery of additional taxa may show that two species are not as closely related as was formerly supposed.

A second method of testing biogeographical conclusions is to test hypotheses that are based on distributional data. For example, the distributions of species of _E. detersa_ group, and those of small mammals, within the Great Basin, suggest that during the Wisconsinan piñon-juniper woodland was widespread in the area but ponderosa pine and fir forests in the various mountain ranges within the Great Basin were not connected to each other, nor were they connected to those in the mountain ranges that surround the Great Basin. Species associated with piñon-juniper woodland are distributed in the Great Basin where suitable habitat exists while species associated with ponderosa pine and fir forests are essentially absent from the Great Basin, even from mountain ranges that support suitable habitat. The distributional data, however, could be interpreted in a radically different way. It could be assumed that during Wisconsinan time ponderosa pine and fir were sufficiently widespread in the Great Basin to allow species of insects and mammals to reach the mountain ranges within the Basin. At some time during the post-glacial, a period of extreme heat or aridity eliminated the fauna associated with these forests but did not affect the more long-lived tree species. The first hypothesis was selected as being the most probable mainly because relict populations of more species would be expected to have survived on the mountain ranges of the Great Basin if they had formerly occurred there. These opposing hypotheses could be tested in several ways. First, the basic tenet of the first hypothesis, namely the distributional conclusions, could be falsified by discovery of populations of species associated with ponderosa pine forests in the Great Basin. Second, the assumption that these species were prevented from reaching the mountain ranges of the Great Basin because of a lack of suitable habitat in the intermontane lowlands could be falsified by discovery of plant fossils that demonstrate former occurrence of ponderosa pine in the intervening lowlands. Third, the assumption that the fauna associated with ponderosa pine was not present in the Great Basin in Wisconsinan time could be falsified by discovery of fossil remains of this fauna. While it is unlikely that identifiable fossils of species of the *Euxoa detersa* group will ever be found, discovery of mammal fossils in the area would lend credibility to the alternative hypothesis.

Two other examples of distributional data that could falsify or support a conclusion are: discovery of *Euxoa costata* in the Colorado Rockies, or of *E. castanea* in the southern Sierra Nevadas, would cast doubt on conclusions reached regarding distributions of these two species during Wisconsinan time; the discovery of a population of *E. latro* in the southern Rocky Mountains would support the hypothesis that this species reached the La Sal Mountains from the east.

The value of biogeographical hypotheses, in terms of general applicability, must ultimately be assessed by comparisons with other biogeographical analyses. If similar distribution patterns are found in other groups of organisms, and the same kinds of historical explanations can account for distributional similarities and differences, especially with respect to disjunctions, then the credibility of the hypotheses will be improved.

In summary, I draw five general conclusions from this analysis:

1. Great Plains and Great Basin aridlands were isolated from each other during the Wisconsinan glacial maximum.

2. Great Plains aridlands were restricted to several relatively small areas during Wisconsinan time; Great Basin aridlands were less affected than were those of the Great Plains.

3. Ponderosa pine and fir forests were not widespread in the

Great Basin during Wisconsinan time.

4. More Great Basin aridland taxa invaded the Great Plains during the post-glacial than the converse.

5. During Wisconsinan time, species associated with pine, fir spruce and aspen forests were widespread in the mountain ranges of western North America and in most of the Great Plains region south of the ice sheet.

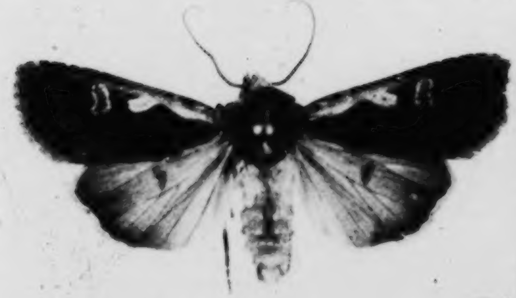
6. Concluding Remarks

An interesting and perplexing array of problems is presented to taxonomists and ecologists by the genus Euxoa. The large number of species and available names, structural uniformity among species, and extensive intraspecific variability, all contribute to the difficulties of taxonomic revision. These difficulties are further compounded by the occurrence of similar patterns of geographical variation in wing markings and color being duplicated in a number of species. Also, the number of documented examples of interspecific hybridization has been increasing steadily.

The problems that make Euxoa difficult, however, also serve to make it particularly interesting biologically. A group of experimental taxonomists in Ottawa have been studying Euxoa for a number of years and have been attempting to analyse taxonomic problems from a variety of different approaches (see review of this by Hudson, 1973). Their findings have contributed greatly to a better understanding of the nature of these problems. It is hoped that data from these studies will help solve some of the problems in our knowledge of the phylogenetic relationships in Euxoa.

Ecological studies of Euxoa species are hampered by two factors: the large number of species that can occur together; an inability to identify larvae. If characters cannot be found by which larvae can be identified, it may be possible to study test plots of larvae in the field or laboratory, then rear them to adults and obtain accurate identifications and bionomic data in this way. Such information would greatly improve our knowledge of resource partitioning and geographical distribution in Euxoa species. Information on habitat specificity would also be invaluable for biogeographical studies.

Figs. 1-8. Adults of *Euxoa* spp. 1, *E. costata* (Grote), male, Golden, B.C., 2 mi E., 3000 ft; 2, *E. costata* (Grote), female, Radium Hot Springs, B.C., 16 mi N., 2900 ft; 3, *E. castanea* Lafontaine, new species, male holotype, Golden, B.C., 2 mi E., 3000 ft; 4, *E. castanea* Lafontaine, new species, female paratype, Radium Hot Springs, B.C., 16 mi N., 2900 ft; 5, *E. foeminalis* (Smith), male, Prescott, Ariz., 5 mi N., 5450 ft, Yavapai Co.; 6, *E. foeminalis* (Smith), female, Prescott, Ariz., 5 mi N., 5450 ft, Yavapai Co.; 7, *E. idahoensis* (Grote), male, Exshaw, Alta., 5 mi NE., 4225 ft; 8, *E. idahoensis* (Grote), female, Exshaw, Alta., 5 mi NE., 4225 ft. (Specimens reproduced at about 2X).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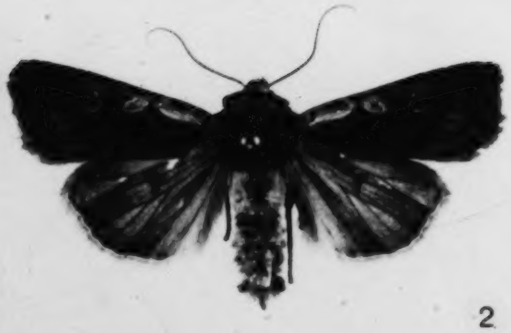
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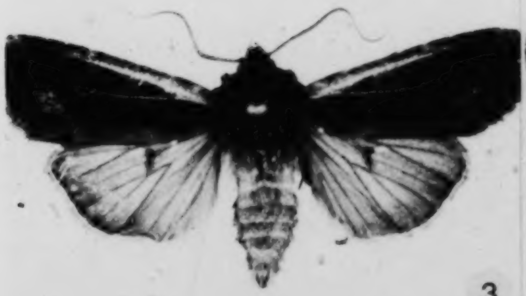
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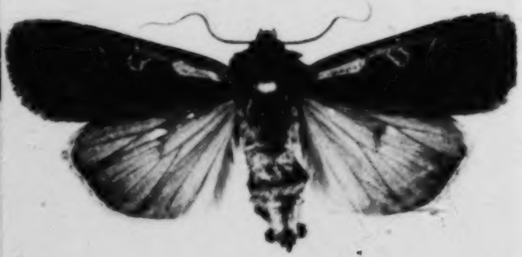
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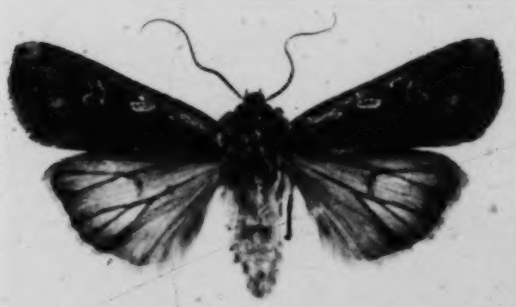
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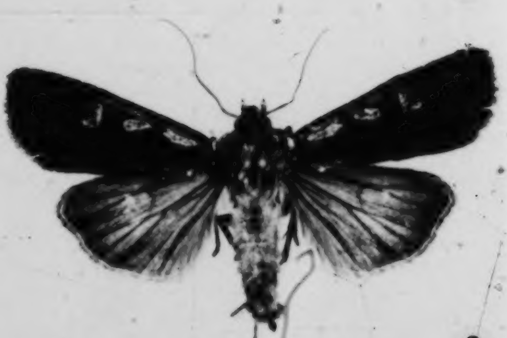
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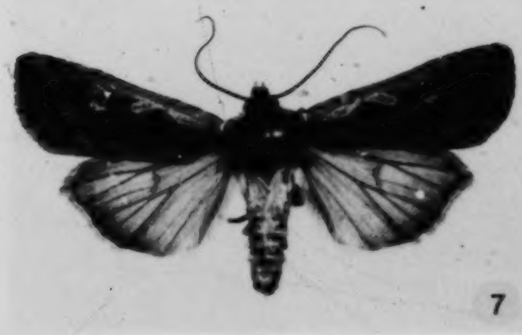
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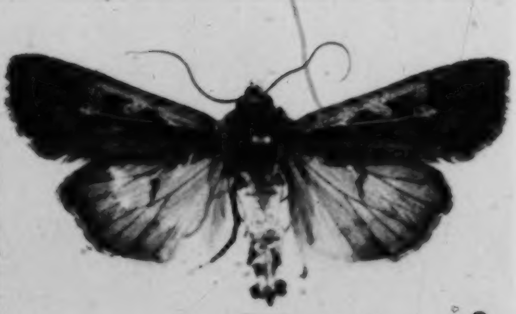
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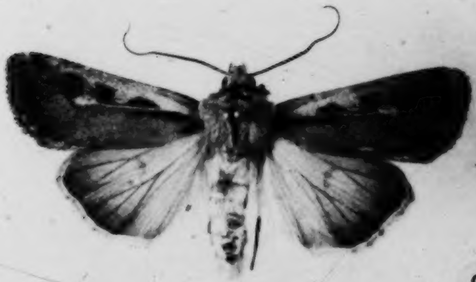
Figs. 9-16. Adults of Euxoa spp. 9, E. idahoensis (Grote), male, Lethbridge, Alta.; 10, E. idahoensis (Grote), male, Radium Hot Springs, B.C., 16 mi N., 2900 ft; 11, E. idahoensis (Grote), male, Eureka, Utah; 12, E. idahoensis (Grote), male, Hill City, Pennington Co., S. Dak.; 13, E. clausa McDunnough, male, Lethbridge, Alta.; 14, E. clausa McDunnough, female, Lethbridge, Alta.; 15, E. brevipennis (Smith), male, McDermitt, Nev., 6 mi W., 4600 ft; 16, E. brevipennis (Smith), female, Warm Springs, Nev., 15 mi ESE., 5300 ft. (Specimens reproduced at about 2X).



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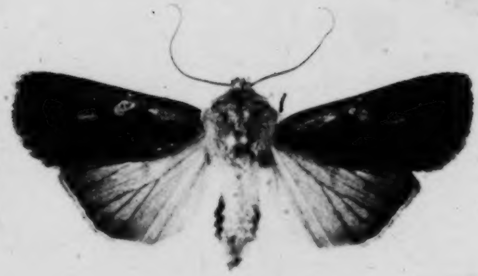

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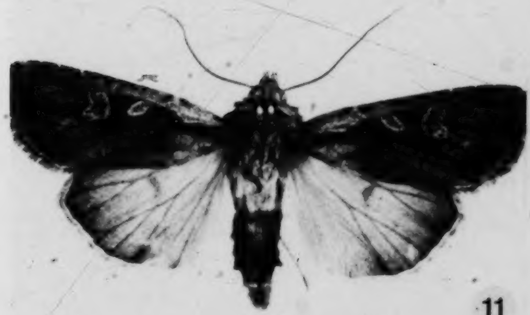

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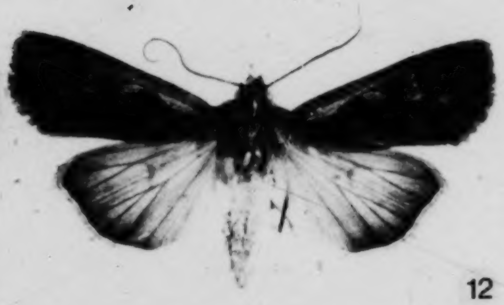

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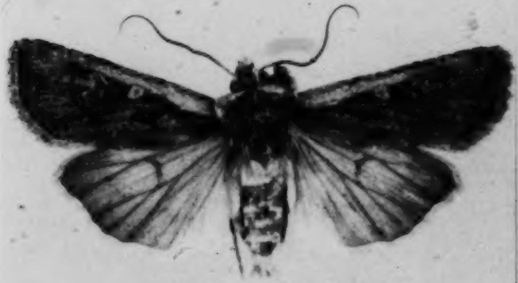

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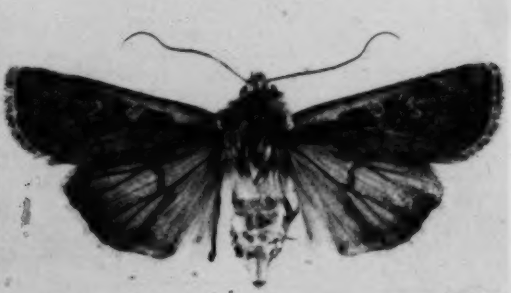

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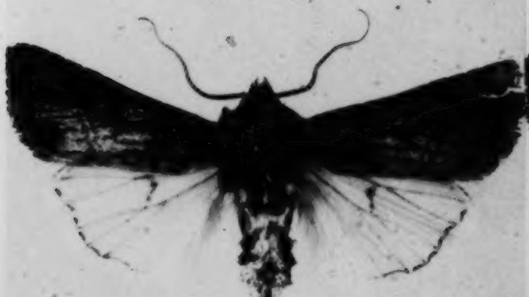

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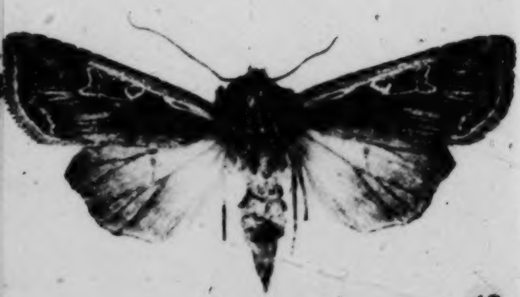

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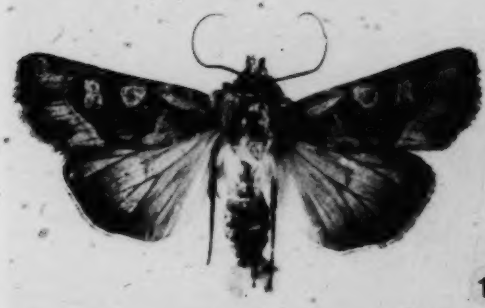
Figs. 17-24. Adults of Euxoa spp. 17, E. servita (Smith), male, Beverley, Sask., 1 mi S., 2400 ft; 18, E. servita (Smith), female, Lloydminster, Alta.; 19, E. servita (Smith), male, Sault St. Marie, Mich.; 20, E. redimicula (Morrison), male, Perth Road, Frontenac Co., Ont.; 21, E. redimicula (Morrison), female, Perth Road, Frontenac Co., Ont.; 22, E. auripennis Lafontaine, male paratype, Choteau, Mont., 10 mi NW., 4050 ft; 23, E. auripennis Lafontaine, female, Leavenworth, Wash., 9 mi NW., 2200 ft; 24, E. arizonensis Lafontaine, female paratype, Greer, White Mts., Apache Co., Ariz., 8500 ft. (Specimens reproduced at about 2X).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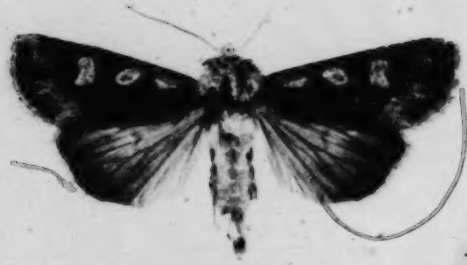
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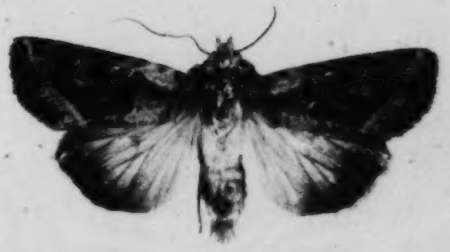
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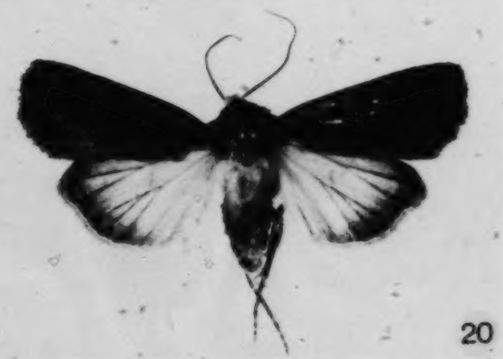
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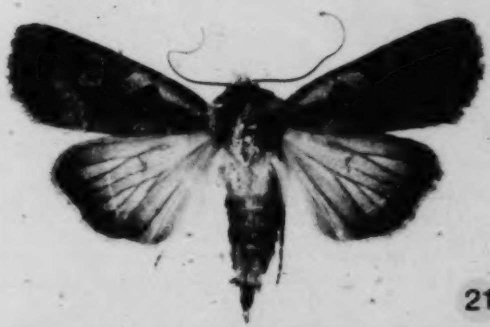
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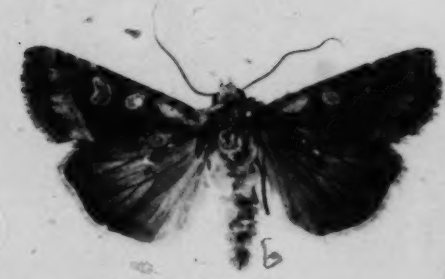
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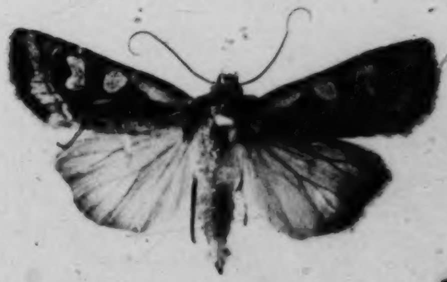
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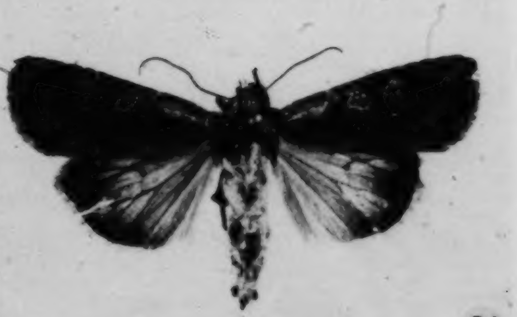
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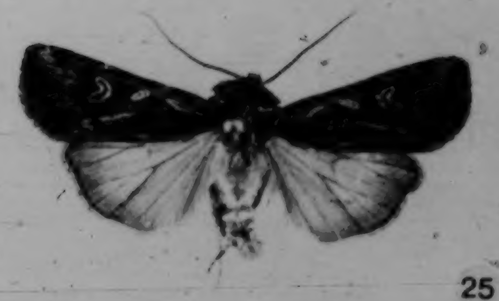
Figs. 25-32. Adults of *Euxoa* spp. 25, *E. olivalis* (Grote), male, Mt. Evans, Colo., 9800 ft; 26, *E. olivalis* (Grote), female, McGaffey, Zuni Mts., McKinley Co., N. Mex., 7500 ft; 27, *E. olivalis* (Grote), female, Lee Vining, Calif., 7 mi WSW., 9600 ft; 28, *E. agema* (Strecker), male, Gallatin Gateway, Mont., 43 mi S., 6700 ft; 29, *E. agema* (Strecker), male, Seneca, Ore., 4.5 mi NW., 4800 ft; 30, *E. oblongistigma* (Smith), male, Eastend, Sask., 2 mi WSW., 3200 ft; 31, *E. oblongistigma* (Smith), male, Laramie, Wyo., 8 mi SE., 8400 ft; 32, *E. oblongistigma* (Smith), female, Ovando, Mont., 5 mi W., 4000 ft. (Specimens reproduced at about 2X).



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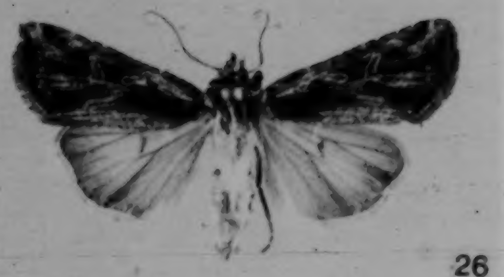

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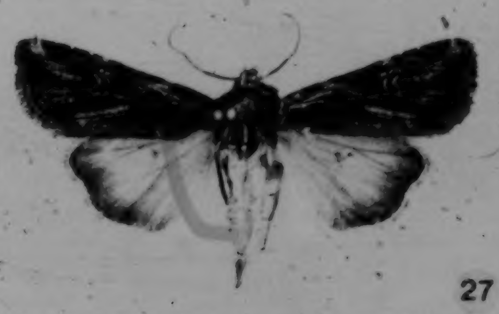

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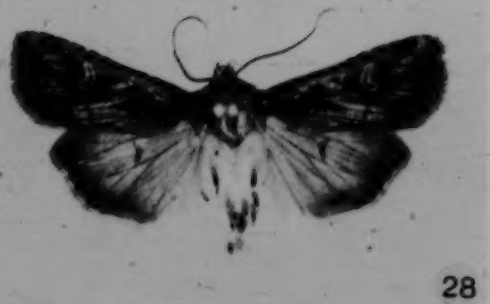

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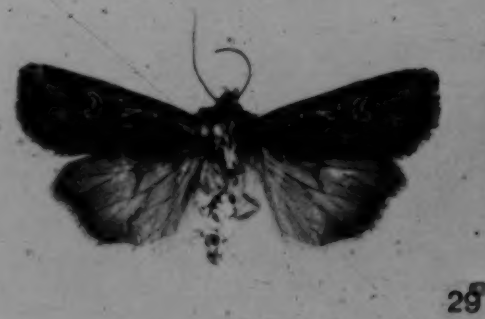

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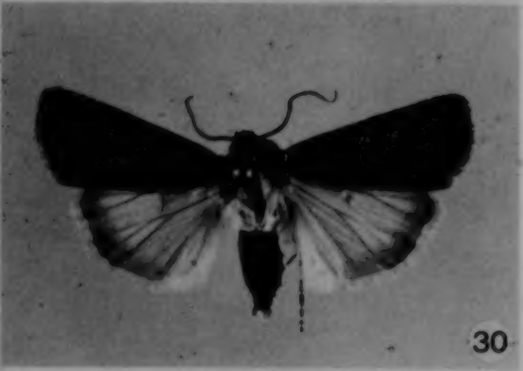

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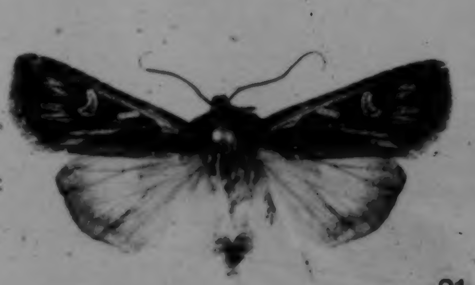

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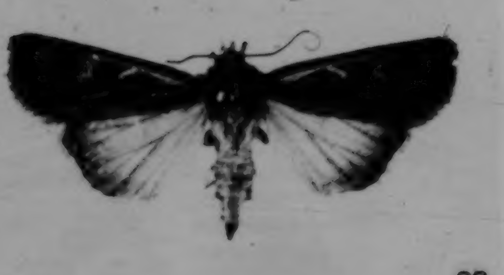

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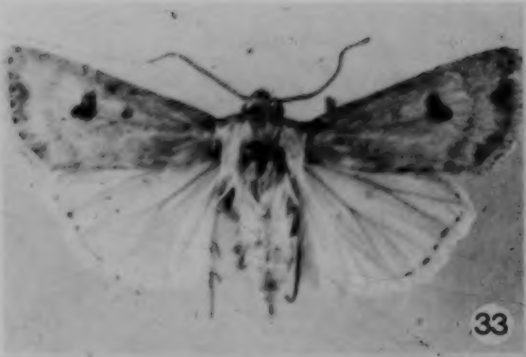
Figs. 33-40. Adults of *Euxoa* spp. 33, *E. citricolor* (Grote), male, Fallon, Nev., 11 mi W., 4100 ft; 34, *E. citricolor* (Grote), male, McDermitt, Nev., 6 mi W., 4600 ft; 35, *E. citricolor* (Grote), female, Walsenberg, Colo., 2 mi W., 6500 ft; 36, *E. tronella* (Smith), Tempiute, Nev., 6 mi SSW., 5600 ft; 37, *E. tronella* (Smith), male, Badlands Nat. Mon., 6 mi NW. Interior, S. Dak., 2300 ft; 38, *E. tronella* (Smith), female, Eureka, Utah, 11 mi NW., 5800 ft; 39, *E. teleboa* (Smith), male, Sand Springs, Mont., 3100 ft; 40, *E. teleboa* (Smith), female, Capulin Nat. Mon., 6 mi SW. Folsom, N. Mex., 7300 ft. (Specimens reproduced at about 2X).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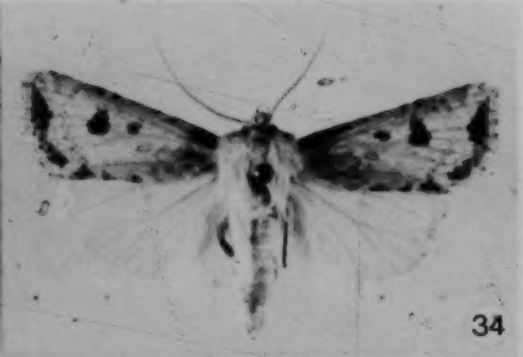
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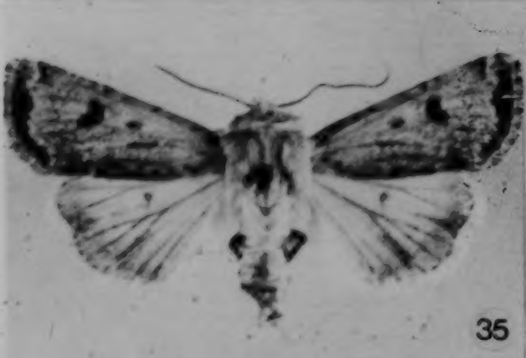
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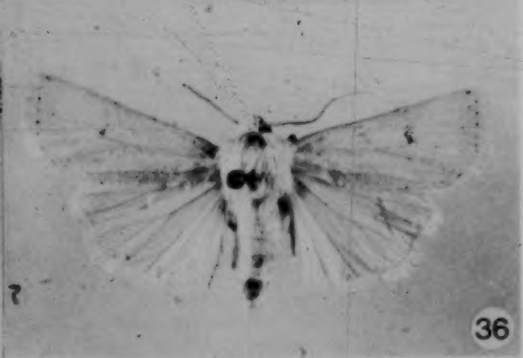
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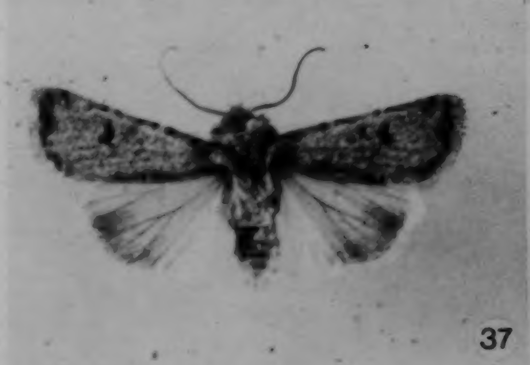
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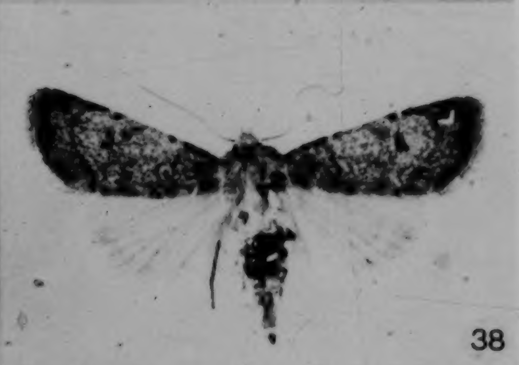
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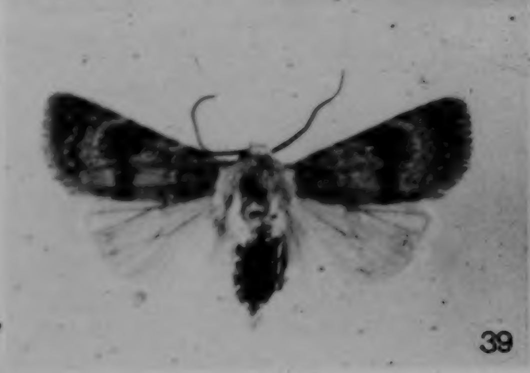
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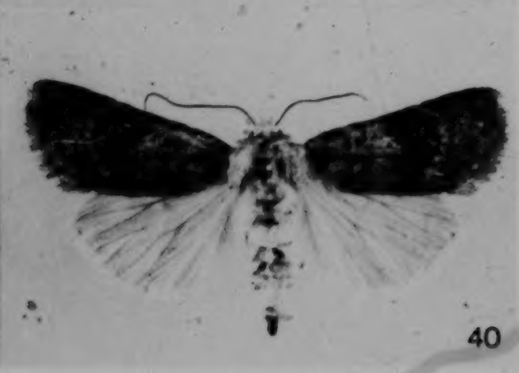
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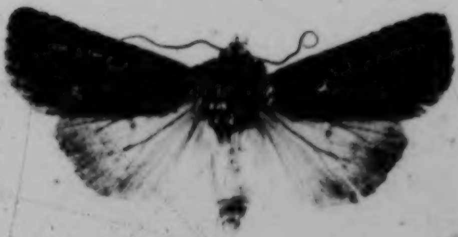
Figs. 41-48. Adults of _Euxoa_ spp. 41, _E. moerens_ (Grote), male, Austin, Nev., 2 mi SE., 7600 ft; 42, _E. moerens_ (Grote), male, Lukachukai, Ariz., 13 mi SE., 7300 ft; 43, _E. moerens_ (Grote), male, Ely, Nev., 5 mi SW., 7400 ft; 44, _E. latro_ (Barnes and Benjamin), male, Chiloquin, Ore., 21 mi N., 4500 ft; 45, _E. latro_ (Barnes and Benjamin), female, Big Bear City, Calif., 6 mi S., 6600 ft; 46, _E. murdocki_ (Smith), male, Yakima, Wash., 20 mi NW., 2100 ft; 47, _E. dodi_ McDunnough, male, Sand Springs, Mont., 1 mi S., 3100 ft; 48, _E. infracta_ (Morrison), female, Radium Hot Springs, B.C., 16 mi N., 2900 ft. (Specimens reproduced at about 2X).



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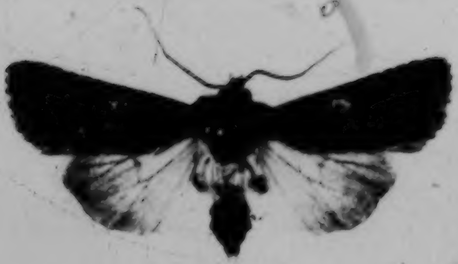

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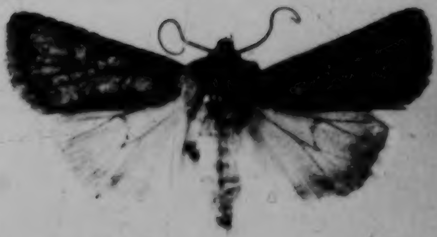

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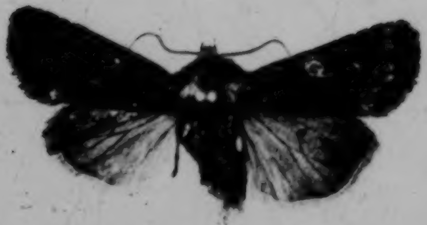

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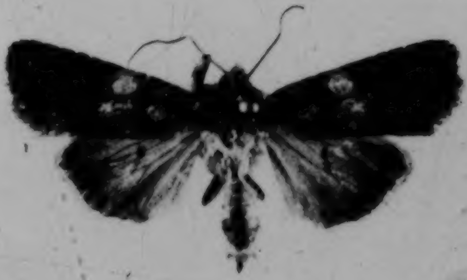

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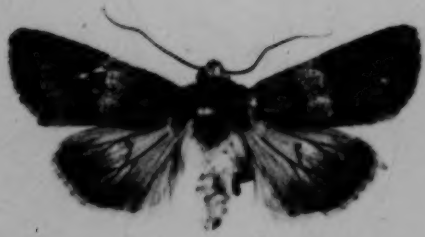

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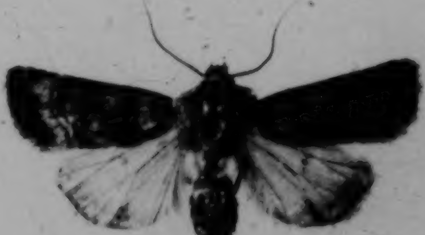

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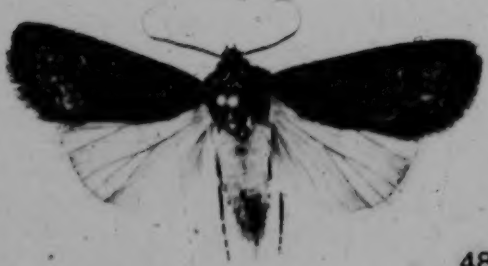

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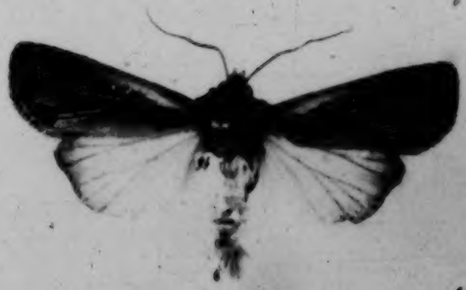
Figs. 49-56. Adults of *Euxoa* spp. 49, *E. laetificans* (Smith), male, Wolf Creek, Mont., 13 mi N., 3800 ft; 50, *E. laetificans* (Smith), female, Wolf Creek, Mont., 13 mi N., 3800 ft; 51, *E. quadridentata* (Grote and Robinson), male, Burns, Ore., 10 mi W., 4300 ft; 52, *E. quadridentata* (Grote and Robinson), female, Follyfarm, Ore., 5 mi SE., 4250 ft; 53, *E. inscripta* Lafontaine, new species, male holotype, Craig, Colo., 22 mi N., 7100 ft; 54, *E. inscripta* Lafontaine, new species, female paratype, Kemmerer, Wyo., 8 mi SW., 6800 ft; 55, *E. niveilinea* (Grote), male, Hugo, Colo., 6 mi NW., 5200 ft; 56, *E. niveilinea* (Grote), male, Capulin Nat. Mon., 6 mi SW., Folsom, N. Mex., 7300 ft. (Specimens reproduced at about 2X).



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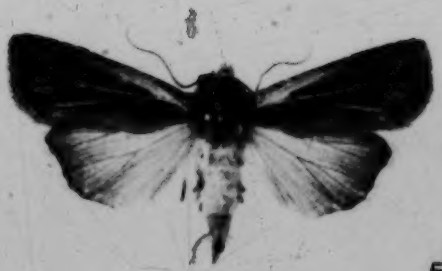

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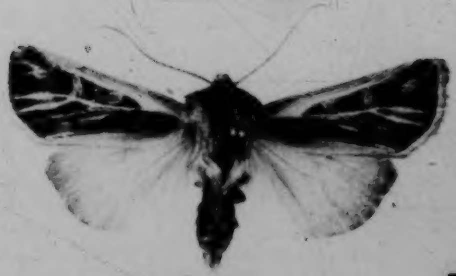

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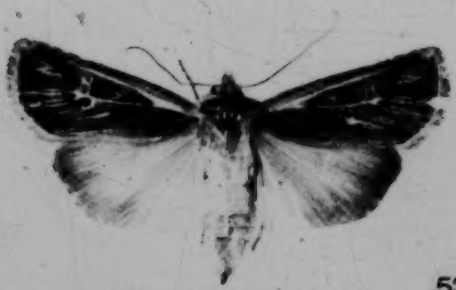

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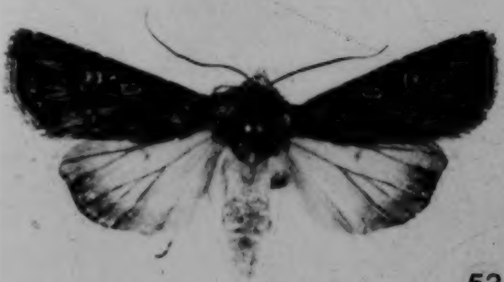

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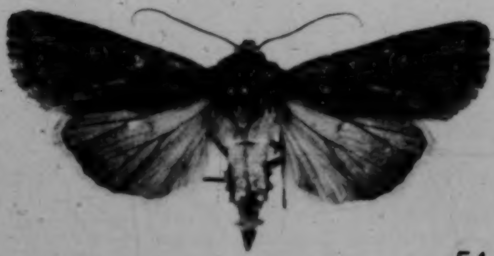

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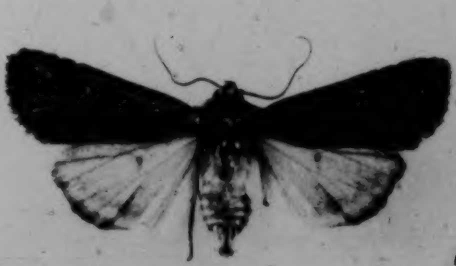

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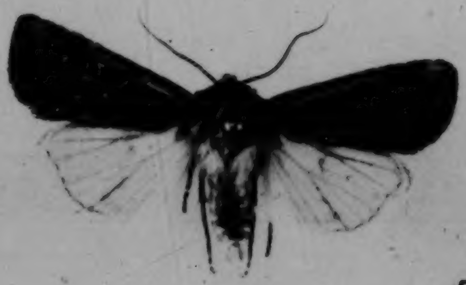
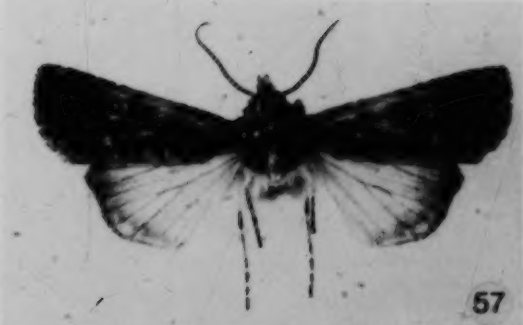


56

Figs. 57-64. Adults of Euxoa spp. 57, E. unica McDunnough, male holotype, Saskatoon, Sask.; 58, E. dargo (Strecker), male, Swift Current, Sask.; 59, E. melura McDunnough, female, Satus Creek, Yakima Co., Wash.; 60, E. d. detersa (Walker), male, E. Wareham, Mass.; 61, E. detersa personata (Morrison), male, Simcoe, Ont.; 62, E. cicatricosa (Grote and Robinson), male, Austin, Nev., 17 mi E., 6600 ft; 63, E. cicatricosa (Grote and Robinson), male, Tonasket, Wash., 8 mi S., 1100 ft; 64, E. recula (Harvey), male, Trona, Calif., 12 mi NNE., 2700 ft. (Specimens reproduced at about 2X).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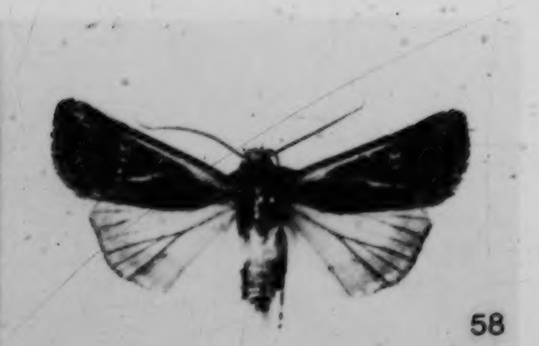
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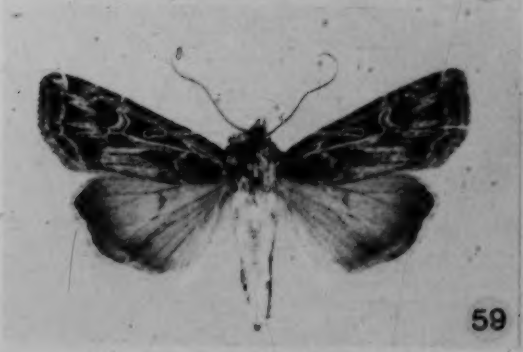
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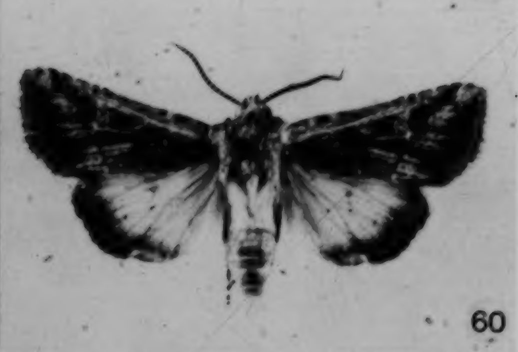
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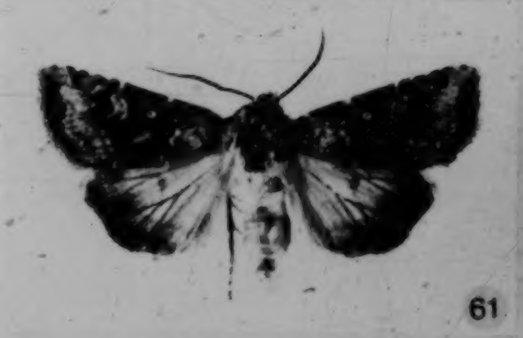
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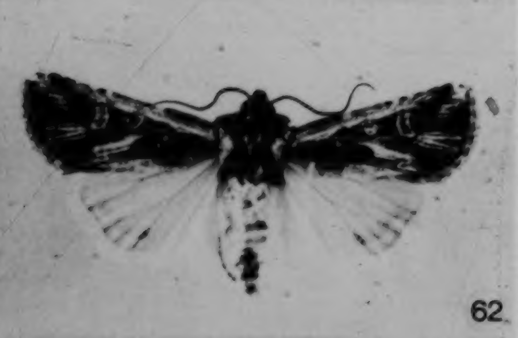
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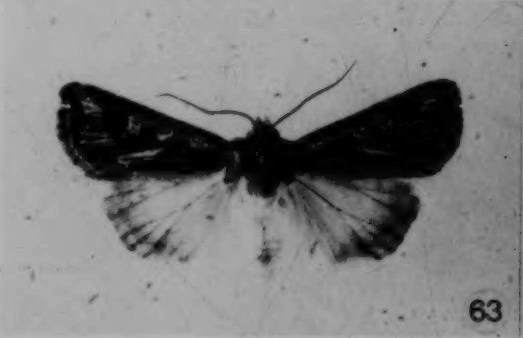
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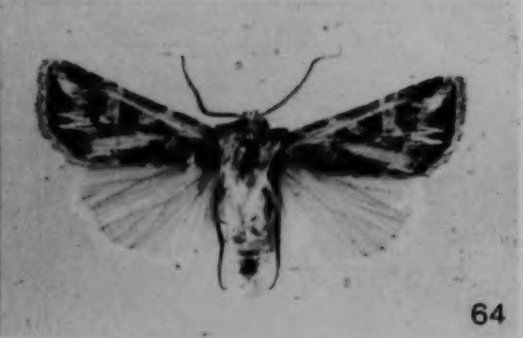
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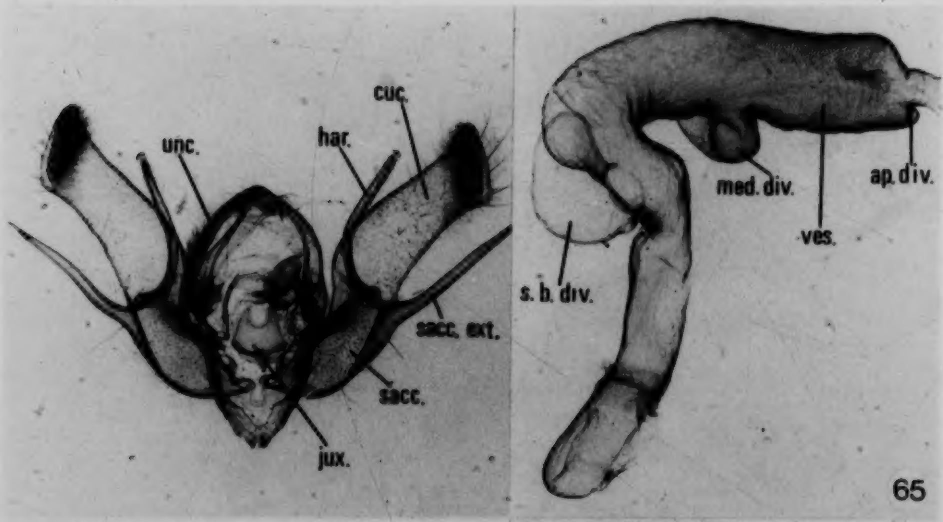
Figs. 65-67. Male genitalia of *Euxoa* spp. (Aedeagus removed and shown at right with vesica everted). 65, *E. costata* (Grt.); 66, *E. castanea* Lafontaine, new species; 67, *E. foeminalis* (Sm.). (Structures reproduced at about 14X). Explanation of abbreviations: unc., uncus; jux., juxta; sacc., sacculus; cuc., cucullus; har., harpe; sacc. ext., sacculus extension; s.b. div., sub-basal diverticulum; med. div., median diverticulum; ves., vesica; ap. div., apical diverticulum.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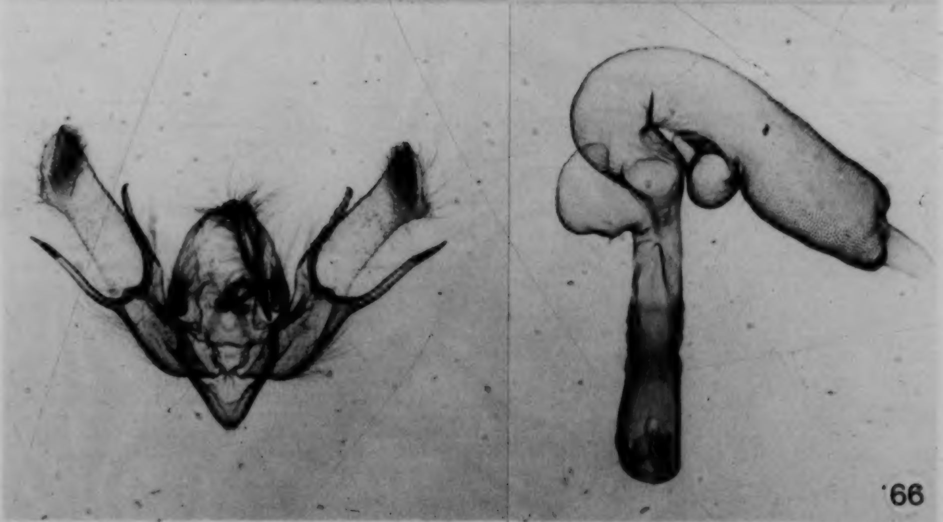

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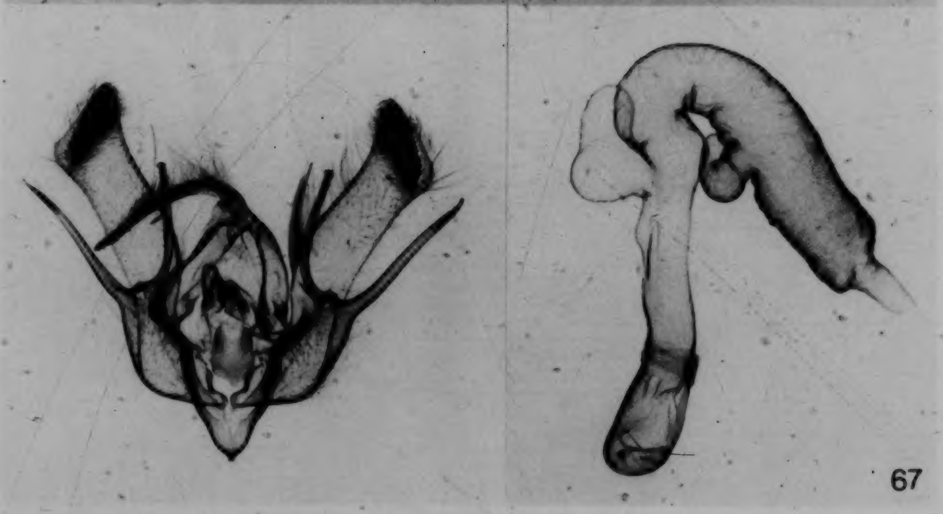
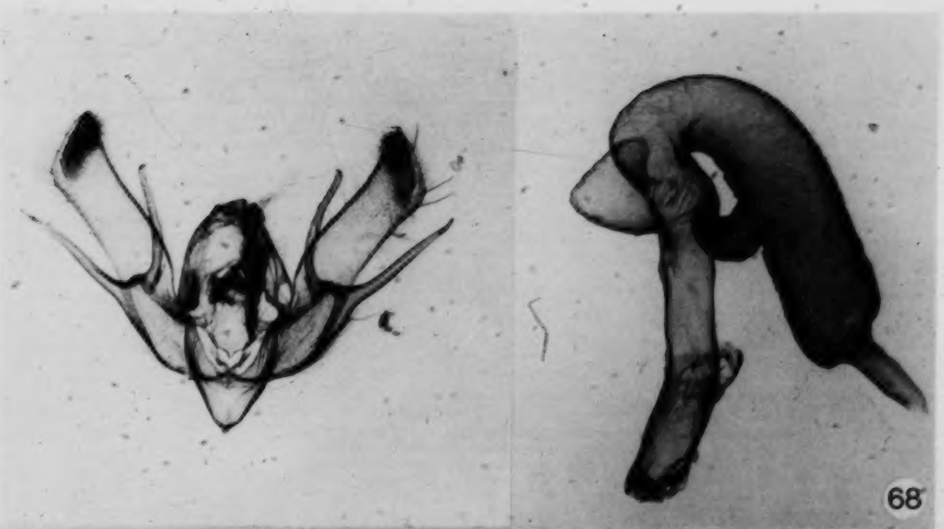


67

Figs. 68-70. Male genitalia of Euxoa spp. (Aedeagus removed and shown at right with vesica everted). 68, E. idahoensis (Grt.); 69, E. clausa McD.; 70, E. brevipennis (Sm.). (Structures reproduced at about 14X).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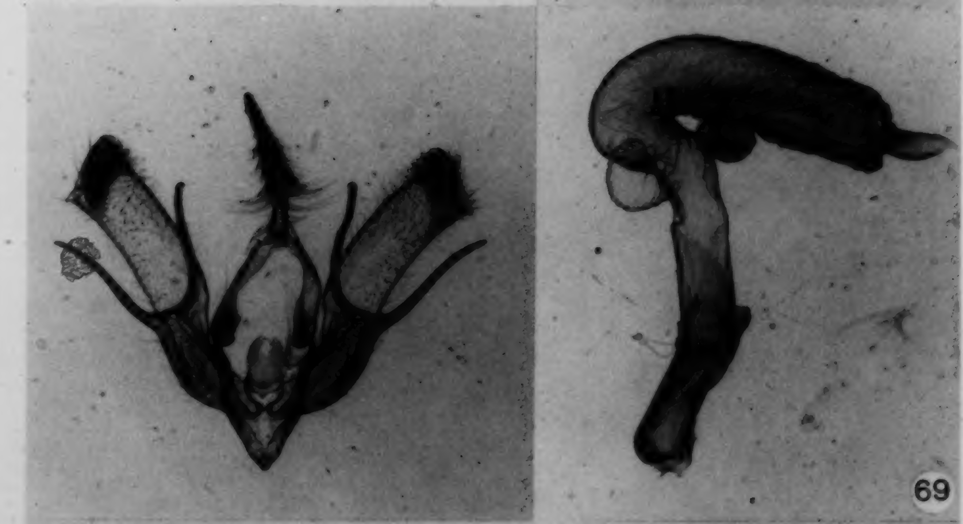
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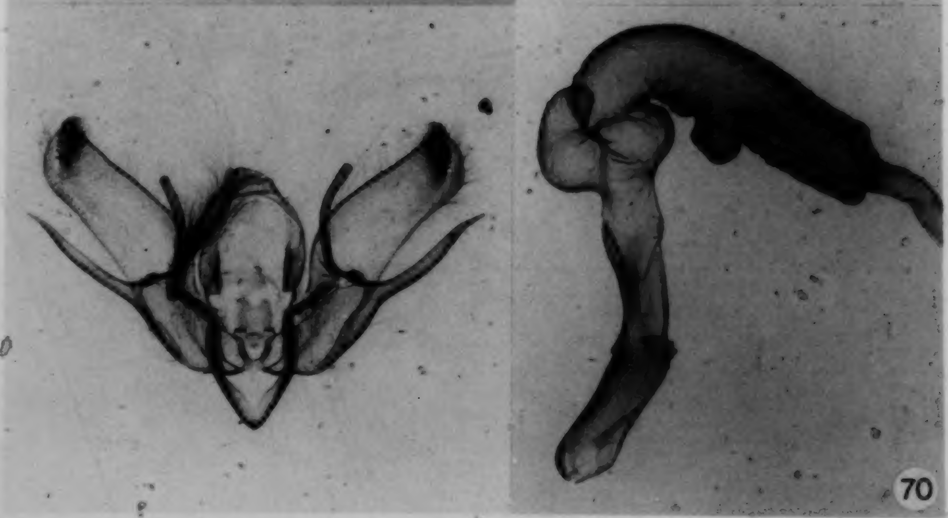
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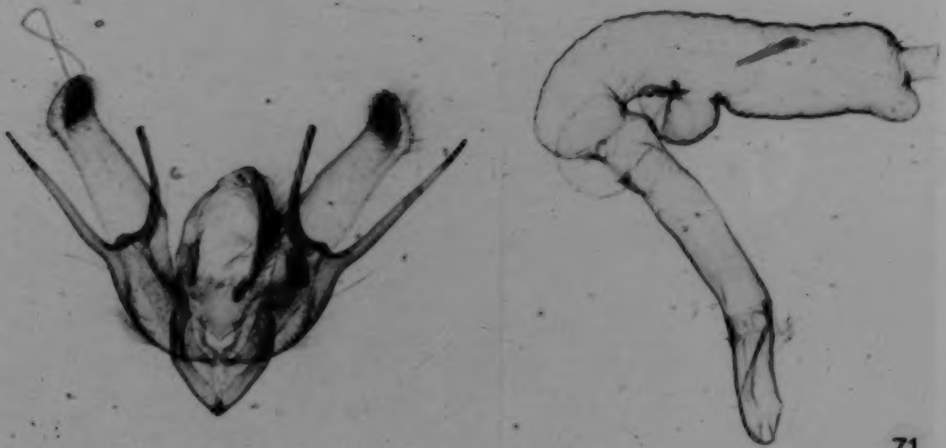
Figs. 71-73. Male genitalia of *Euxoa* spp. (Aedeagus removed and shown at right with vesica everted). 71, *E. servita* (Sm.), 72, *E. redimicula* (Morr.), 73, *E. auripennis* Lafontaine. (Structures reproduced at about 14X).



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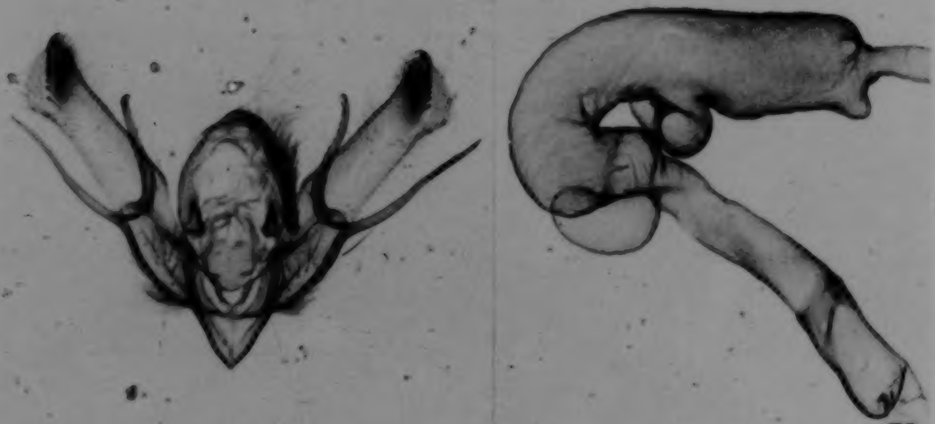

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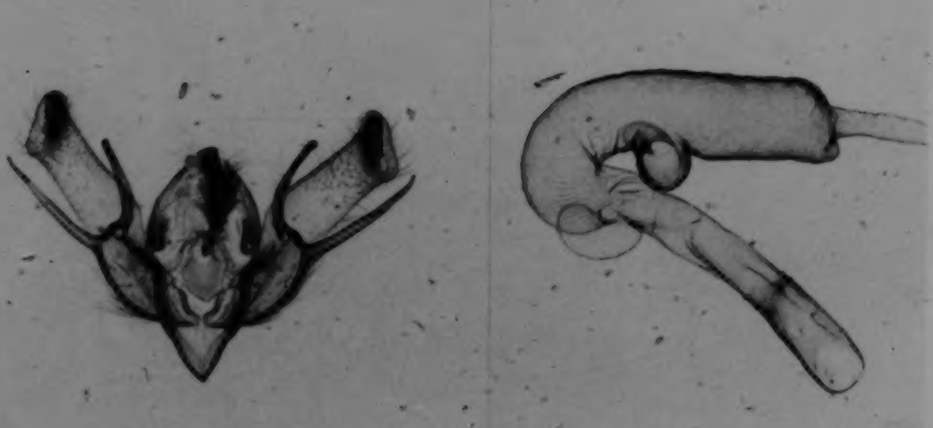

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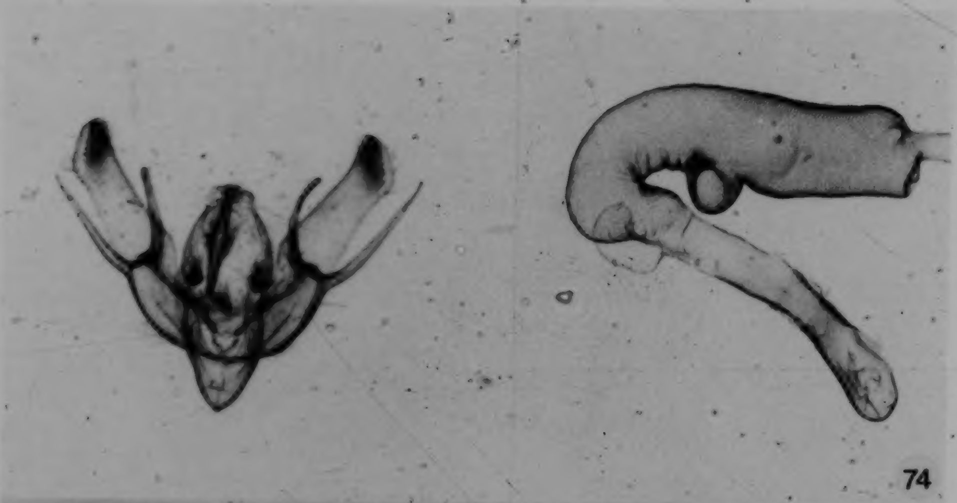
Figs. 74-76. Male genitalia of Euxoa spp. (Aedeagus removed and shown at right with vesica everted). 74, E. arizonensis Lafontaine; 75, E. olivalis (Grt.); 76, E. agema (Stkr.). (Structures reproduced at about 14X).



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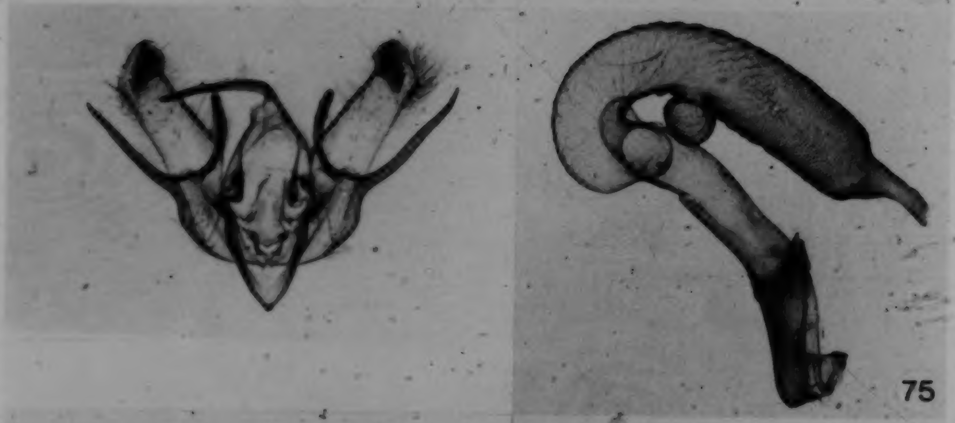

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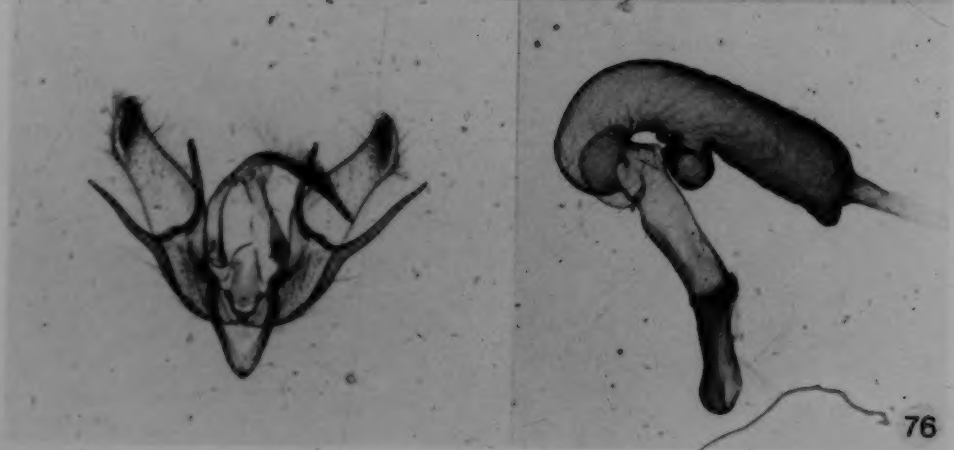

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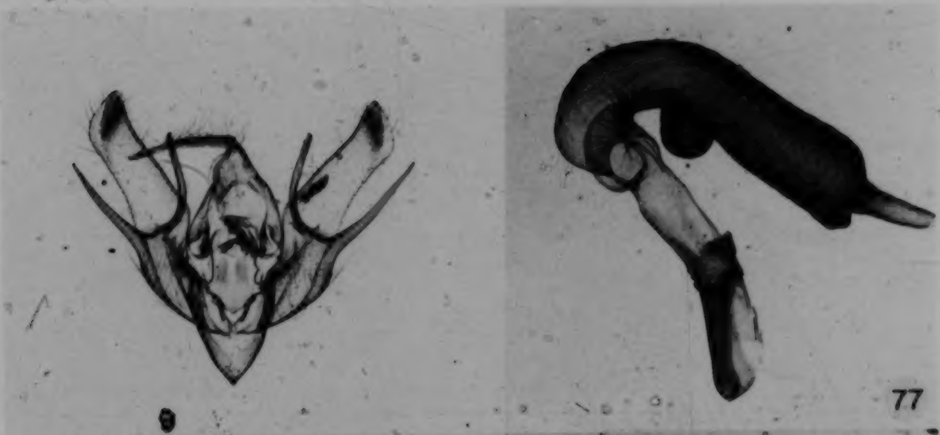
Figs. 77-79. Male genitalia of *Euxoa* spp. (Aedeagus removed and shown at right with vesica everted). 77, *E. oblongistigma* (Sm.); 78, *E. citricolor* (Grt.); 79, *E. tronella* (Sm.). (Structures reproduced at about 14X).



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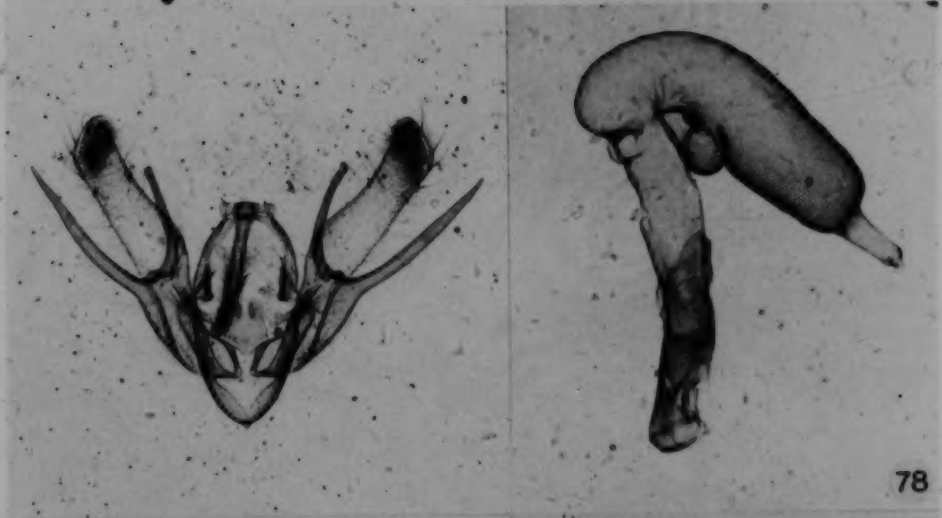

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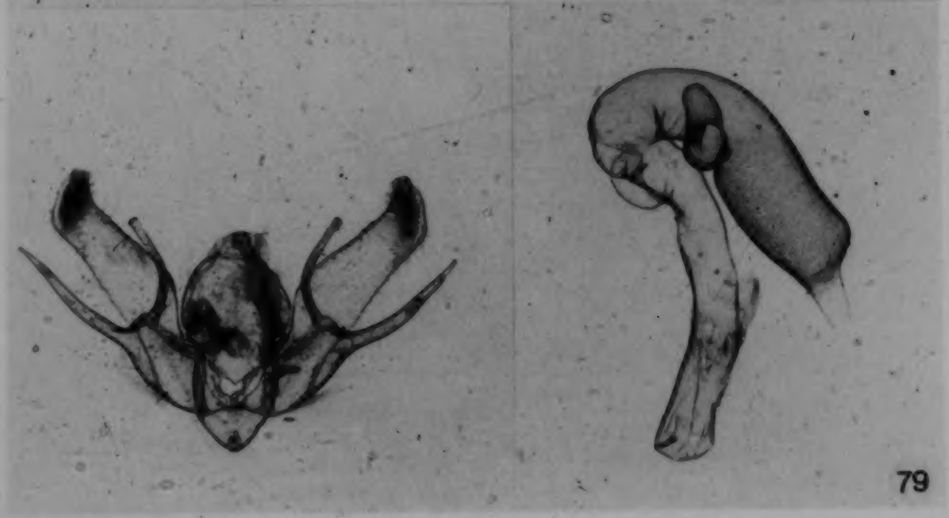

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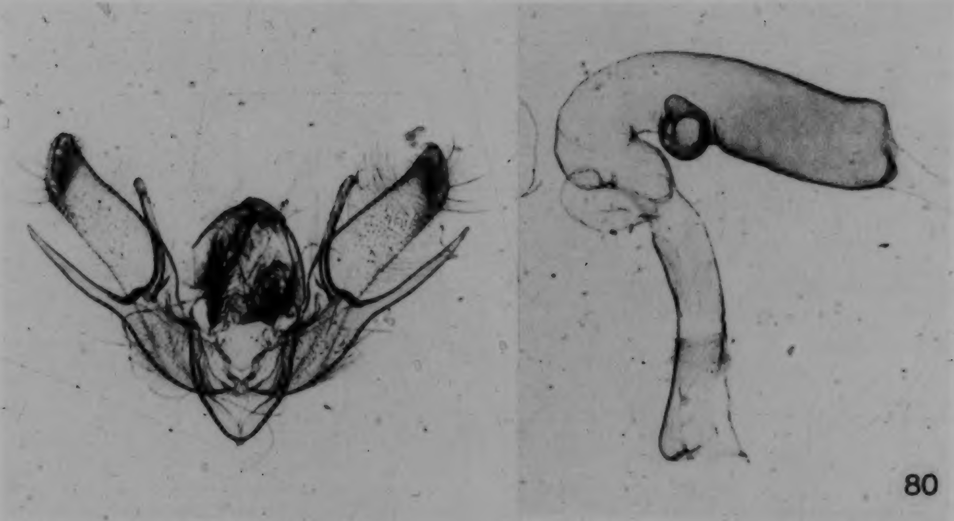
Figs. 80-82. Male genitalia of *Euxoa* spp. (Aedeagus removed and shown at right with vesica everted). 80, *E. teleboa* (Sm.); 81, *E. moerens* (Grt.); 82, *E. latro* (B. & Benj.). (Structures reproduced at about 14X).



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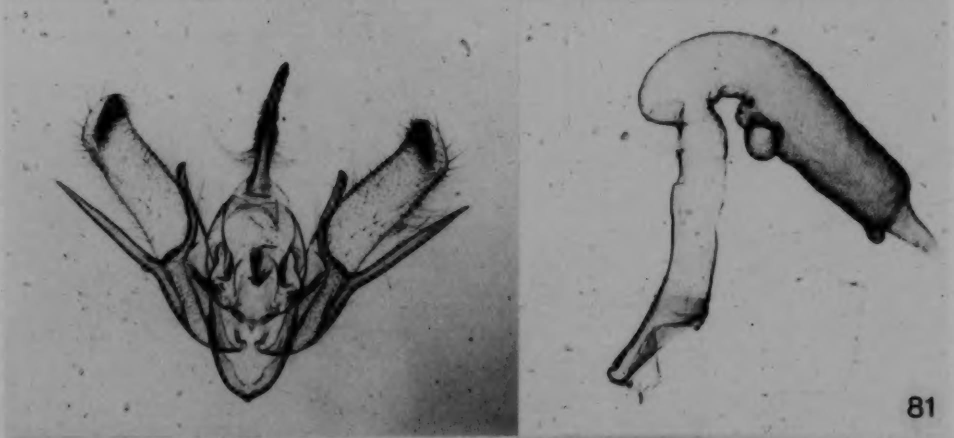

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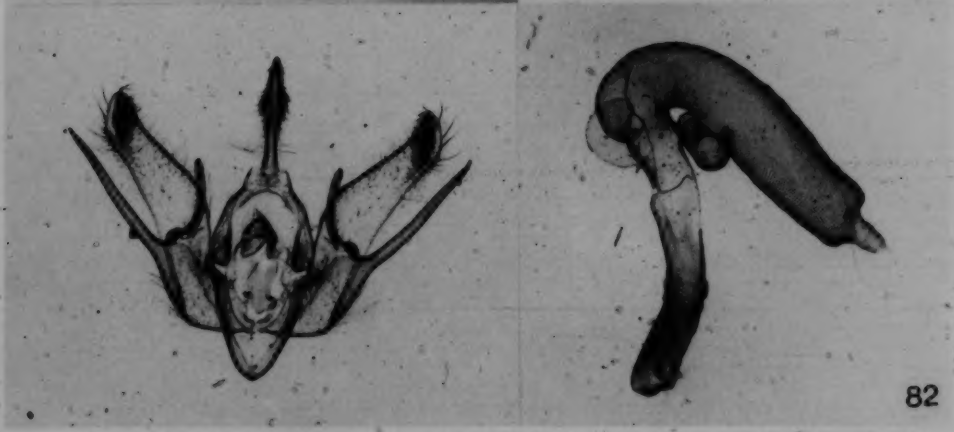

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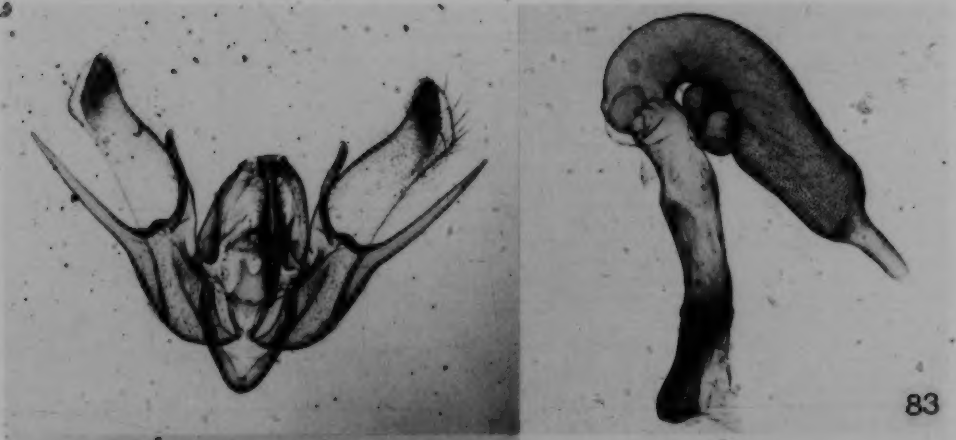
Figs. 83-85. Male genitalia of *Euxoa* spp. (Aedeagus removed and shown at right with vesica everted). 83, *E. murdocki* (Sm.); 84, *E. dodi* McD.; 85, *E. infracta* (Morr.). (Structures reproduced at about 14X).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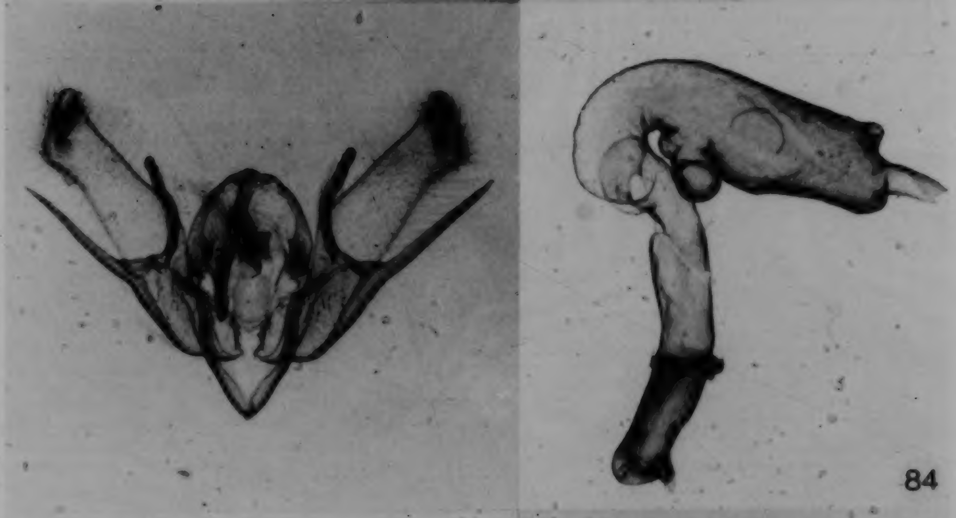
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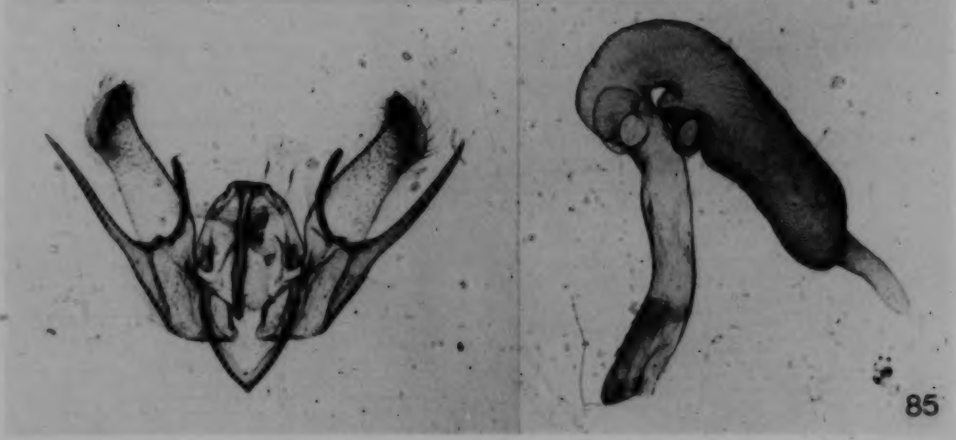
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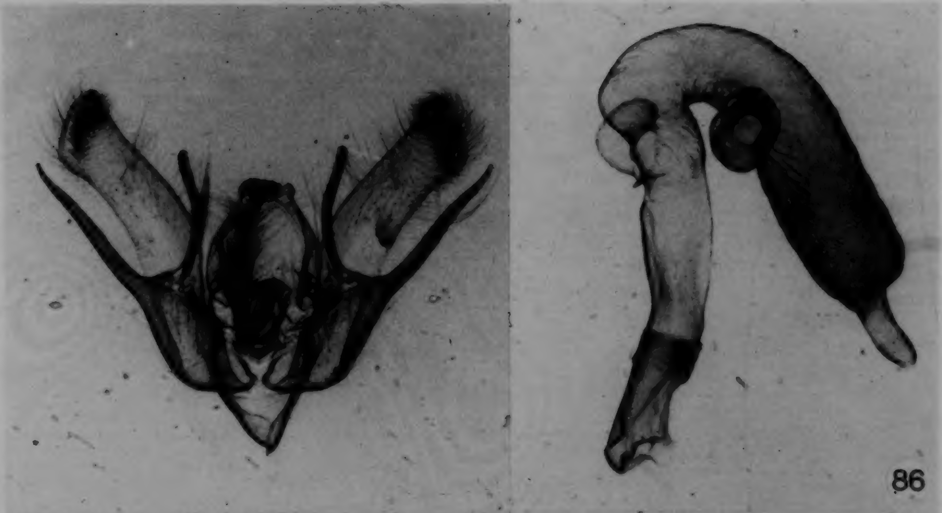
Figs. 86-88. Male genitalia of *Euxoa* spp. (Aedeagus removed and shown at right with vesica everted). 86, *E. laetificans* (Sm.); 87, *E. quadridentata* (Grt. & Rob.); 88, *E. inscripta* Lafontaine, new species. (Structures reproduced at about 14X).



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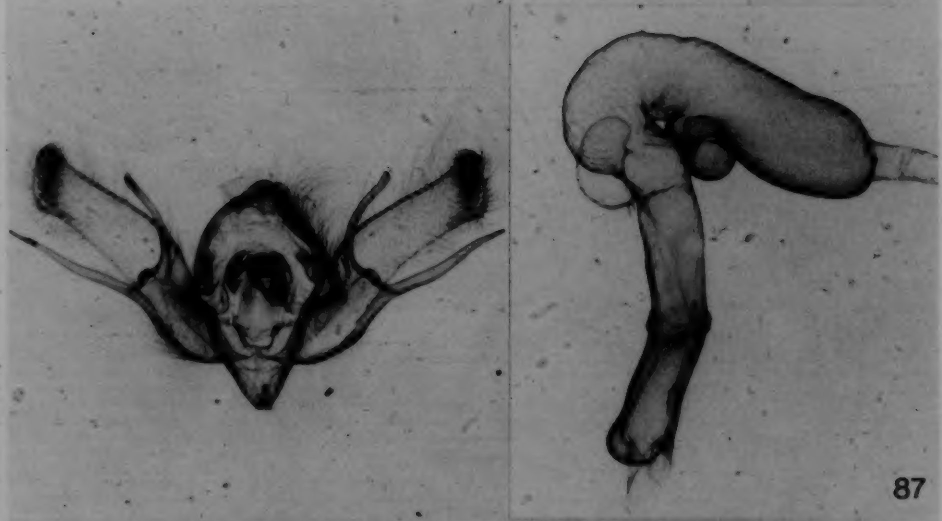

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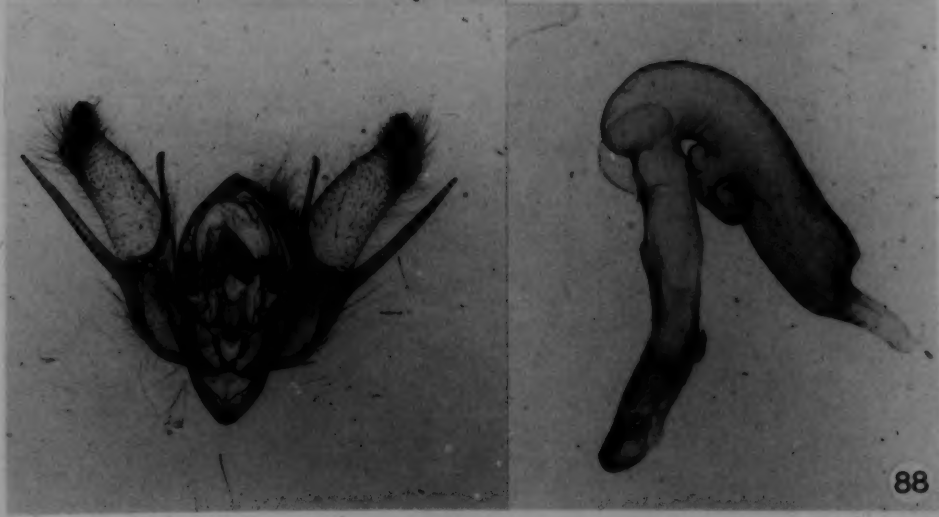

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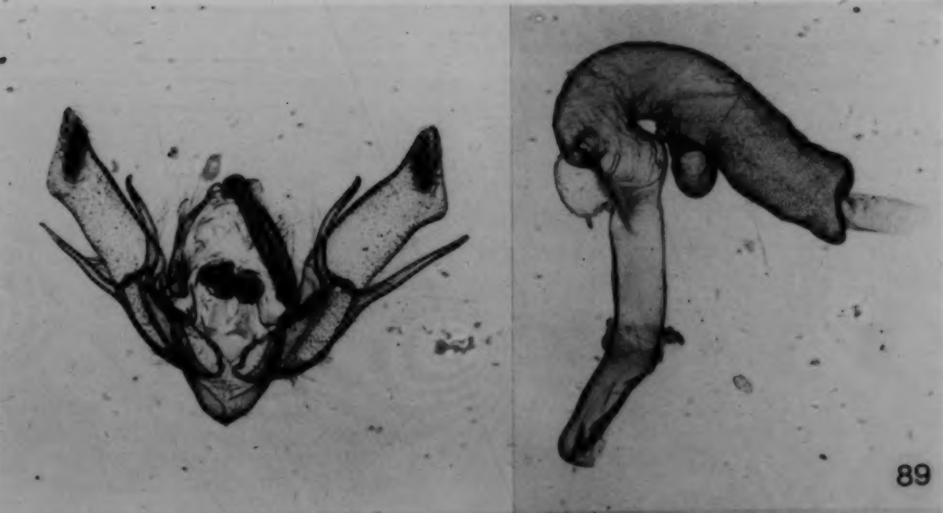
Figs. 89-91. Male genitalia of Euxoa spp. (Aedeagus removed and shown at right with vesica everted). 89, *E. unica* McD.; 90, *E. niveilinea* (Grt.); 91, *E. dargo* (Stkr.). (Structures reproduced at about 14X).



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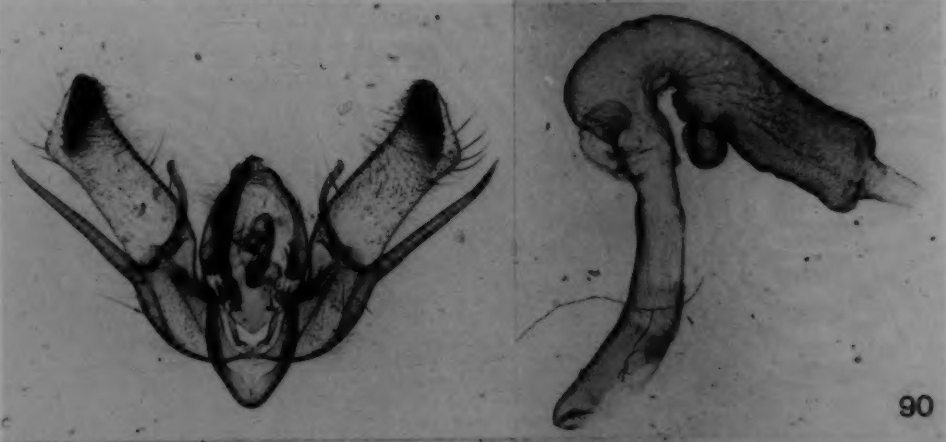

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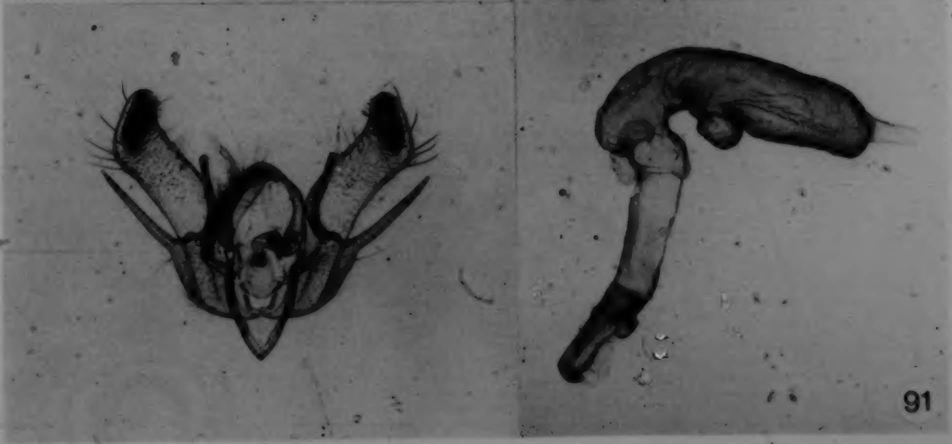

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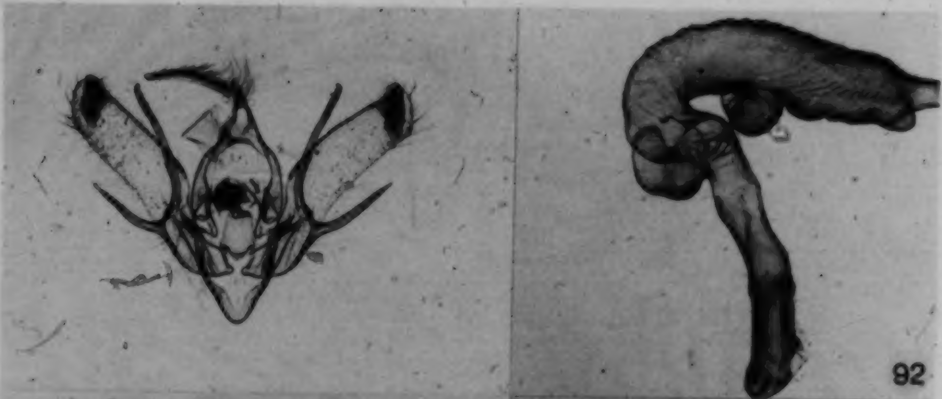
Figs. 92-95. Male genitalia of Euxoa spp. (Aedeagus removed and shown at right with vesica everted). 92, E. melura McD.; 93, E. detersa (Wlk.); 94, E. cicatricosa (Grt. & Rob.); 95, E. recula (Harv.). (Structures reproduced at about 14X).



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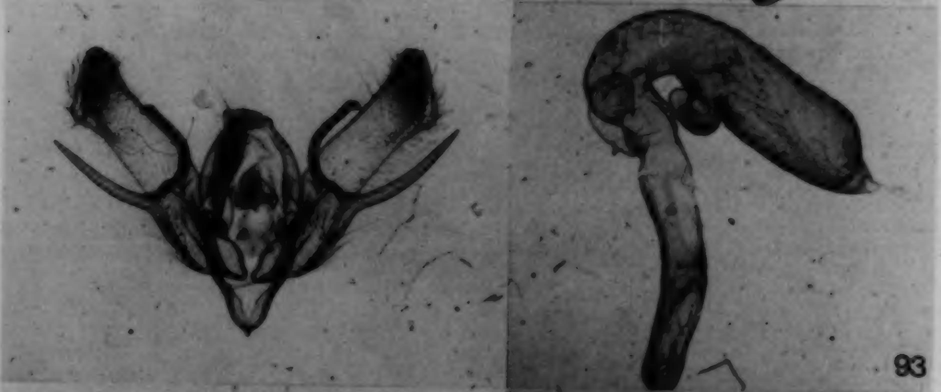

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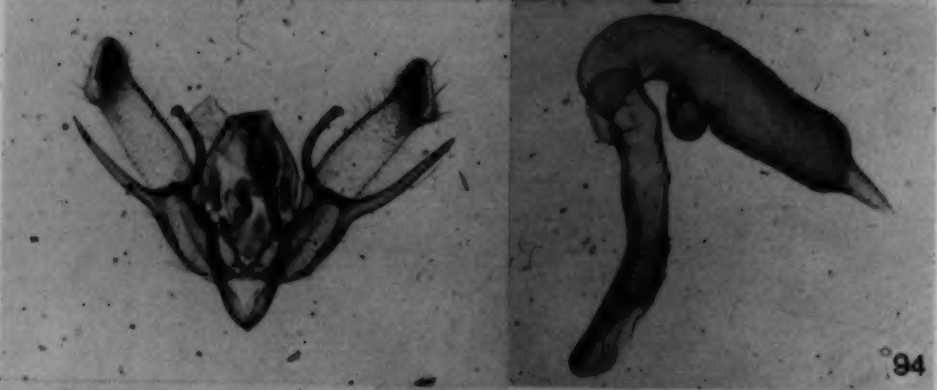

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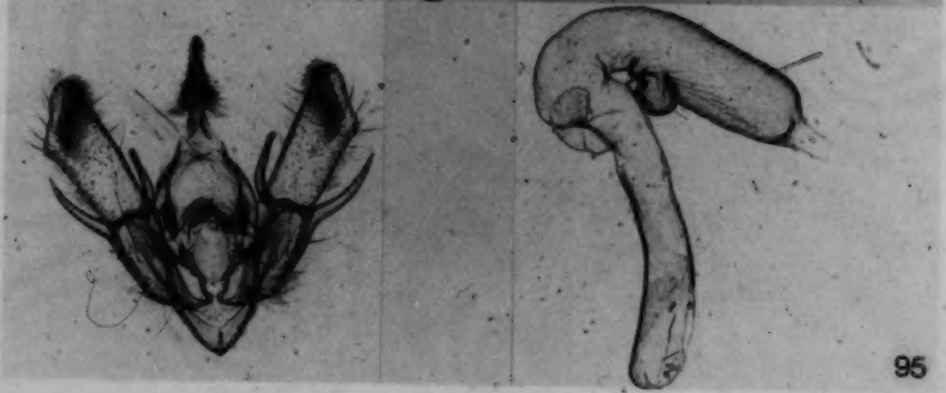

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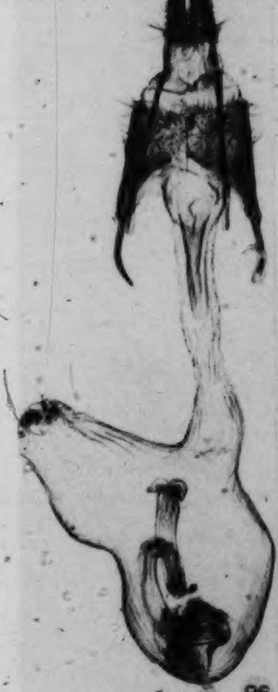
Figs. 96-101. Female genitalia of *Euxoa* spp. 96, *E. costata* (Grt.); 97, *E. castanea* Lafontaine, new species; 98, *E. foeminalis* (Sm.); 99, *E. idahoensis* (Grt.); 100, *E. clausa* McD.; 101, *E. brevipennis* (Sm.). (Structures reproduced at about 9X).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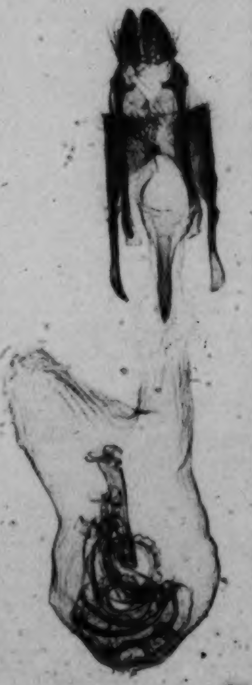
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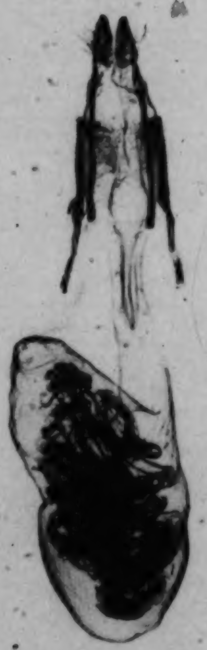
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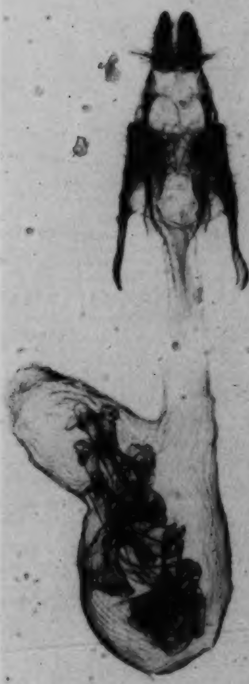
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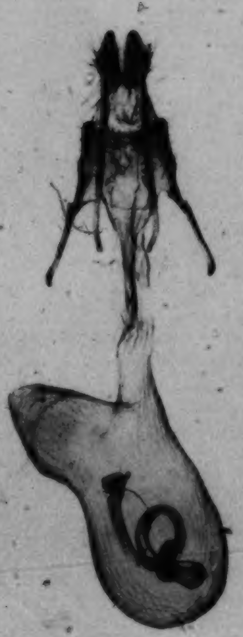
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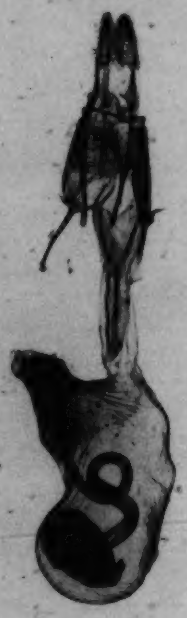
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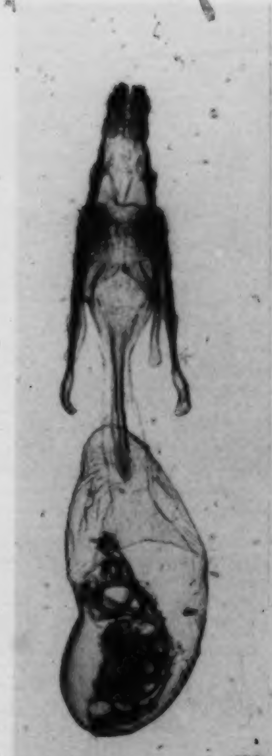
Figs. 102-109. Female genitalia of _Euxoa_ spp. 102, _E. servita_ (Sm.); 103, _E. redimicula_ (Morr.); 104, _E. auripennis_ Lafontaine; 105, _E. arizonensis_ Lafontaine; 106, _E. olivalis_ (Grt.); 107, _E. agema_ (Stkr.); 108, _E. oblogistigma_ (Sm.); 109, _E. citricolor_ (Grt.). (Structures reproduced at about 9X).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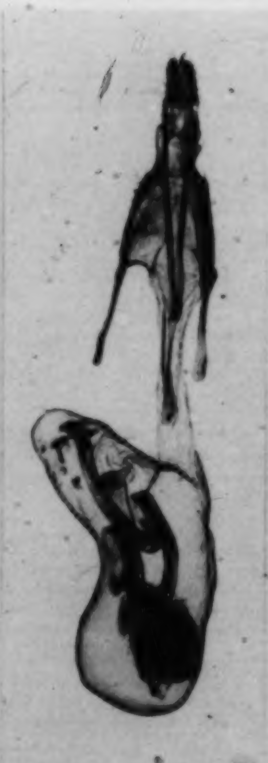
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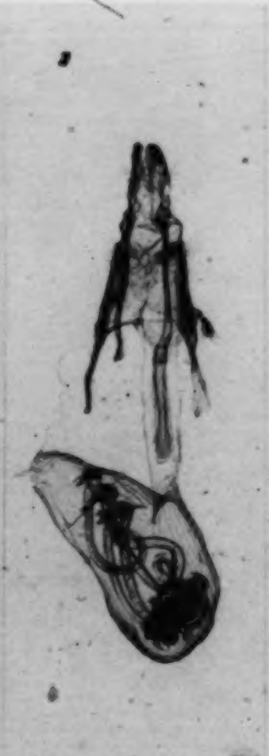
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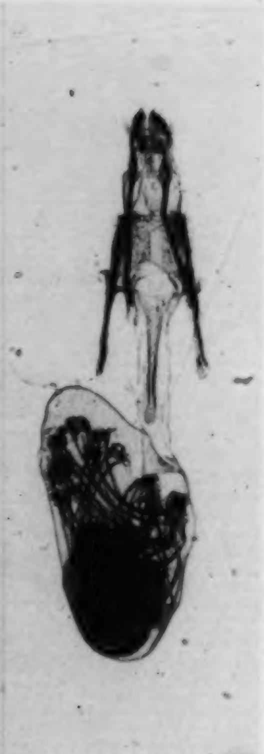
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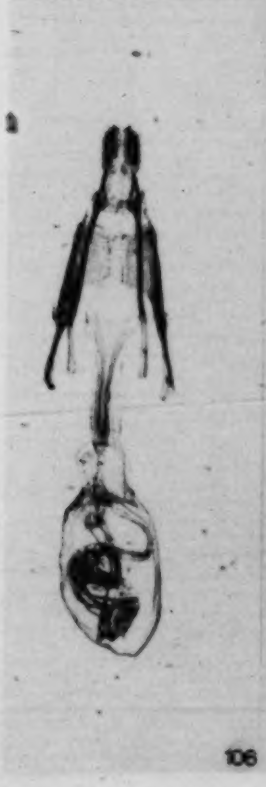
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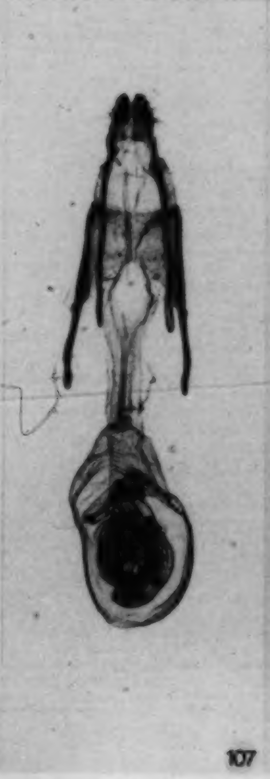
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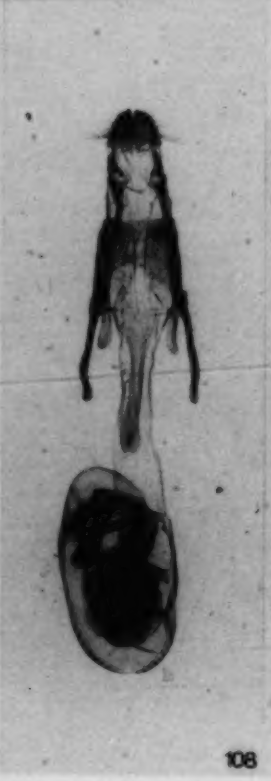
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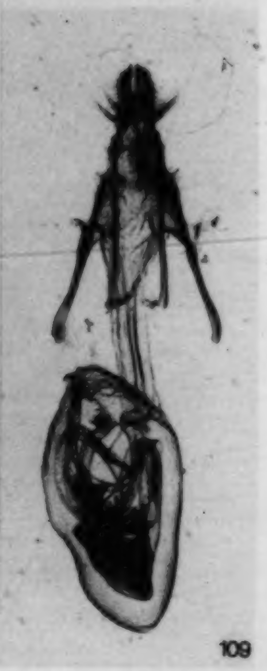
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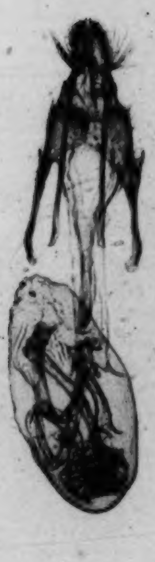
Figs. 110-117. Female genitalia of _Euxoa_ spp. 110, _E._ _tronella_ (Sm.); 111, _E._ _teleboa_ (Sm.); 112, _E._ _moerens_ (Grt.); 113, _E._ _latro_ (B. & Benj.); 114, _E._ _murdocki_ (Sm.); 115, _E._ _dodi_ McD.; 116, _E._ _infracta_ (Morr.); 117, _E._ _laetificans_ (Sm.). (Structures reproduced at about 9X).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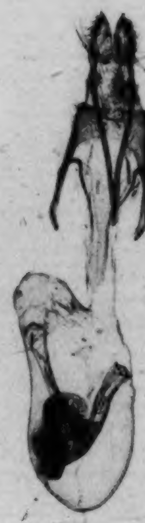
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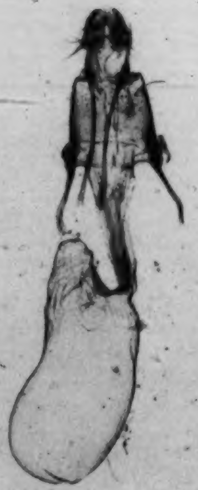
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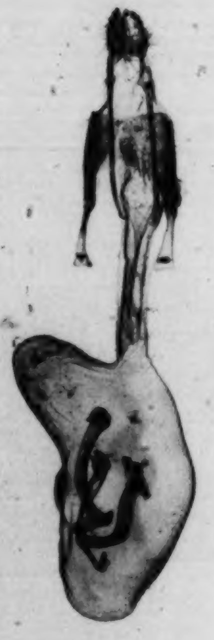
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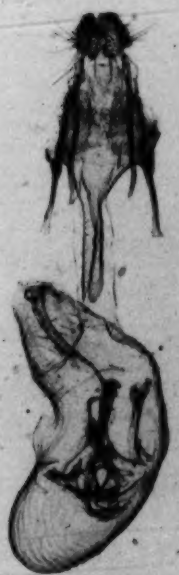
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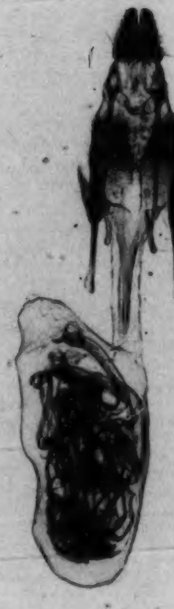
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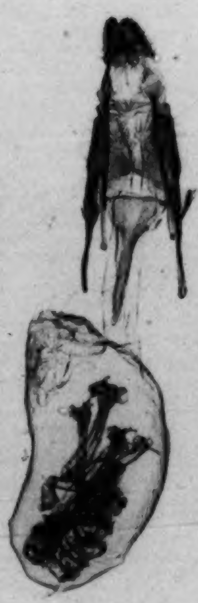
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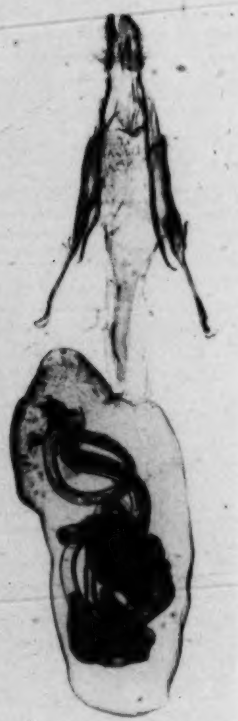
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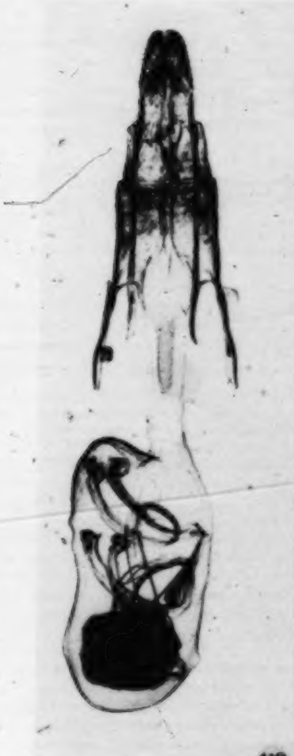
Figs. 118-125. Female genitalia of *Euxoa* spp. 118, *E. quadridentata* (Grt. & Rob.); 119, *E. inscripta* Lafontaine, new species; 120, *E. niveilinea* (Grt.); 121, *E. dargo* (Stkr.); 122, *E. melura* McD.; 123, *E. detersa* (Wlk.); 124, *E. cicatricosa* (Grt. & Rob.); 125, *E. recula* (Harv.). (Structures reproduced at about 9X).



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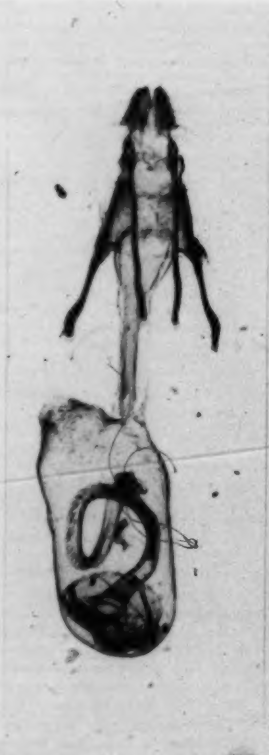

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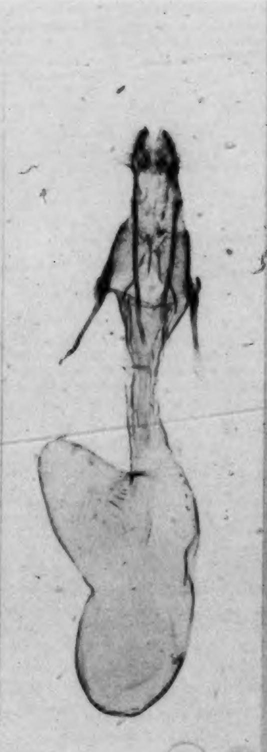

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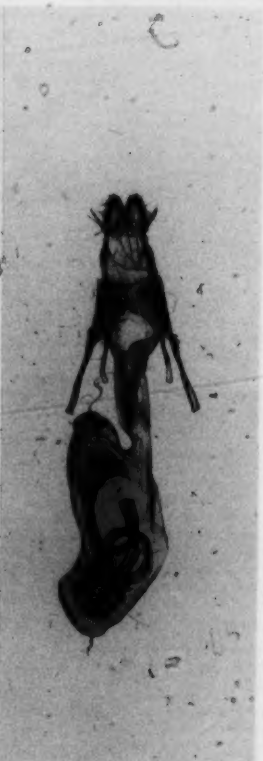

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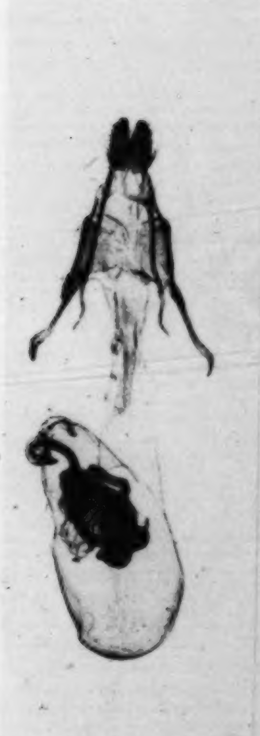

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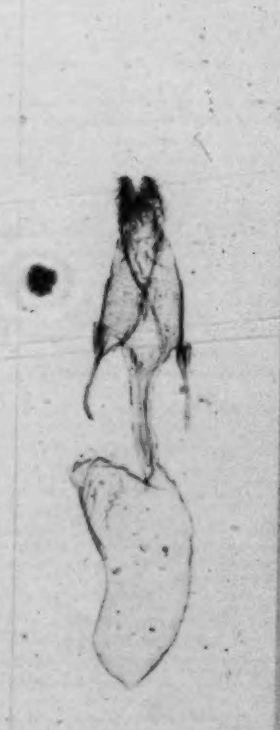

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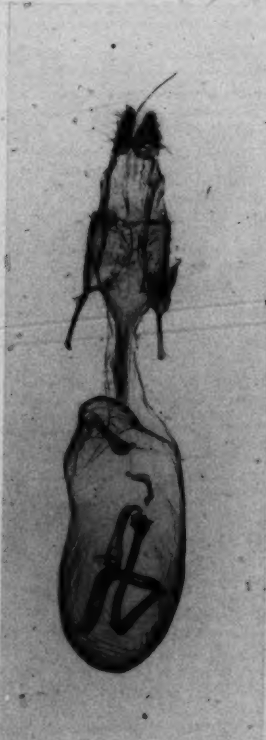

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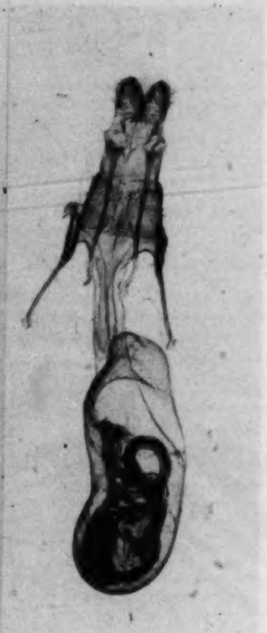
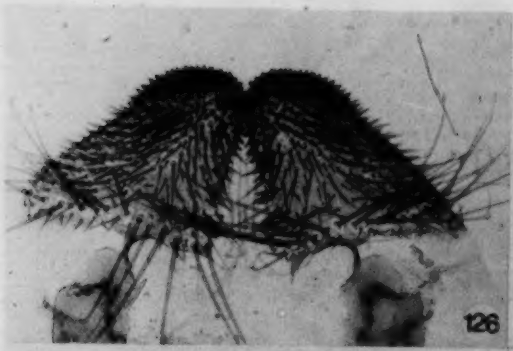


125

Figs. 126-133. Ovipositor valves of _Euxoa_ spp., dorsal aspect. 126, _E. costata_ (Grt.); 127, _E. castanea_ Lafontaine, new species; 128, _E. foeminalis_ (Sm.); 129, _E. idahoensis_ (Grt.); 130, _E. idahoensis_ (Grt.); 131, _E. clausa_ McD.; 132, _E. brevipennis_ (Sm.); 133, _E. servita_ (Sm.). (Structures reproduced at about 32X).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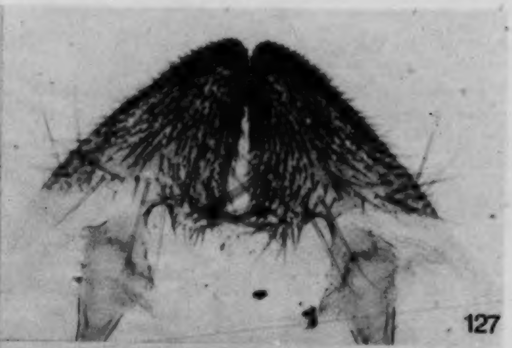
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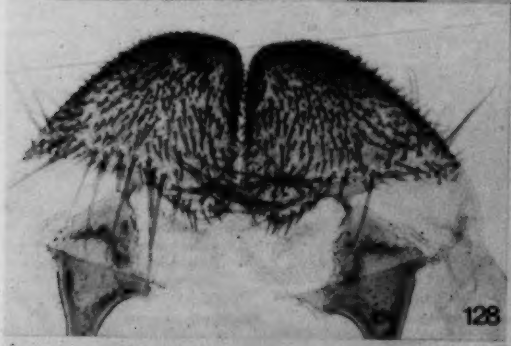
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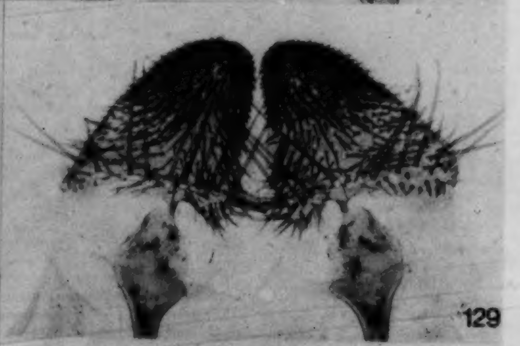
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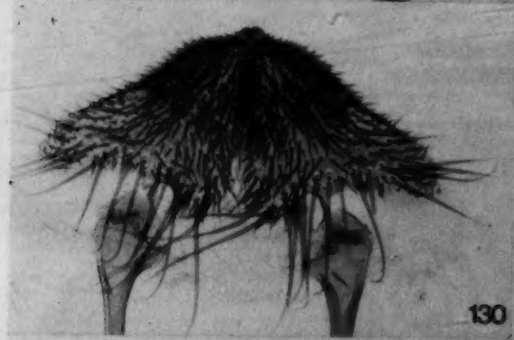
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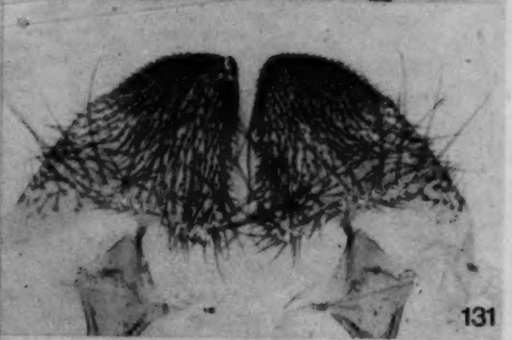
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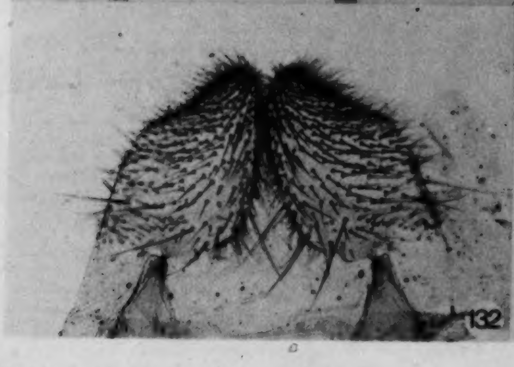
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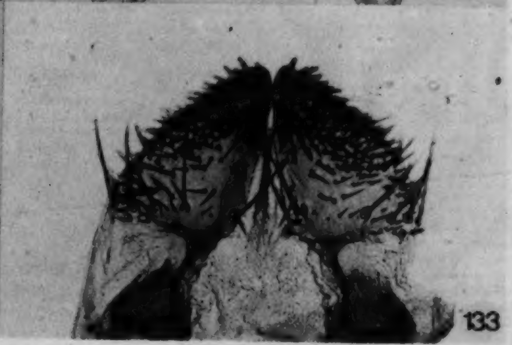
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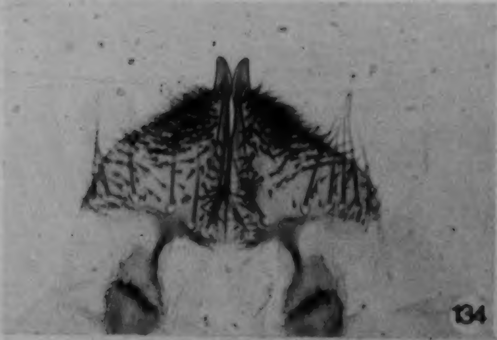
Figs. 134-141. Ovipositor valves of *Euxoa* spp., dorsal aspect. 134, *E. redimicula* (Morr.); 135, *E. auripennis* Lafontaine; 136, *E. arizonensis* Lafontaine; 137, *E. olivalis* (Grt.); 138, *E. agema* (Stkr.); 139, *E. oblongistigma* (Sm.); 140, *E. citricolor* (Grt.); 141, *E. tronella* (Sm.). (Structures reproduced at about 32X).



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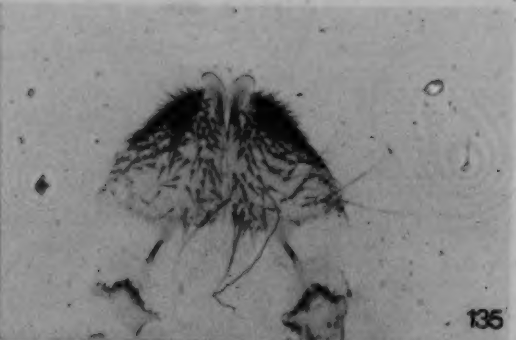

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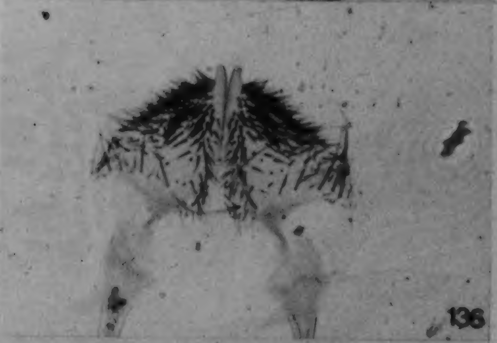

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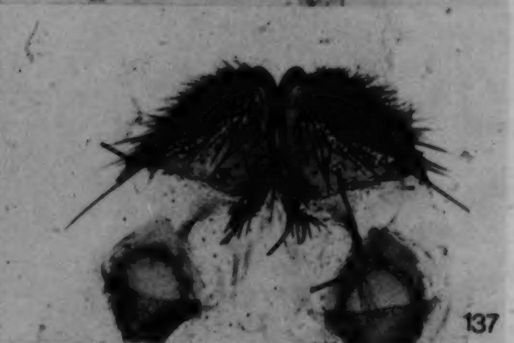

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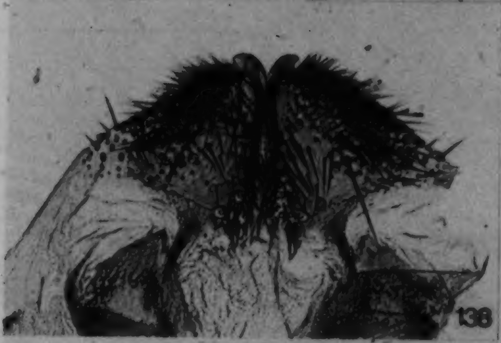

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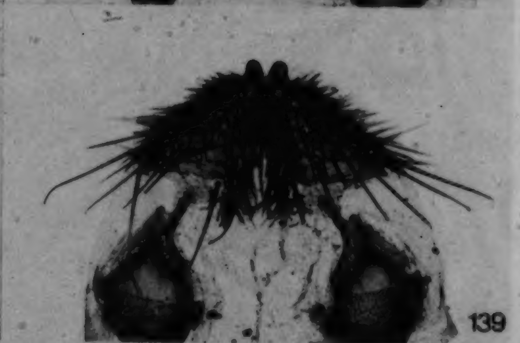

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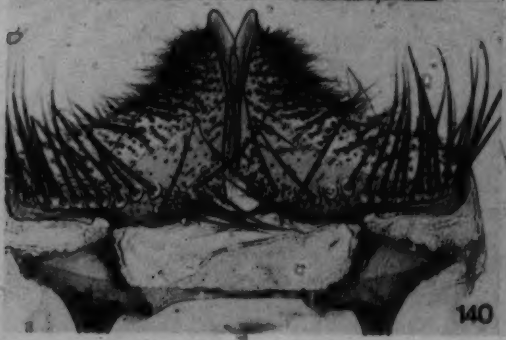

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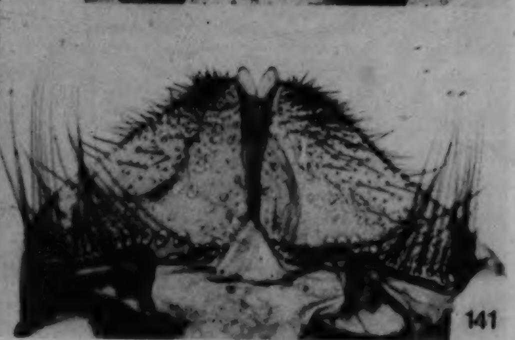

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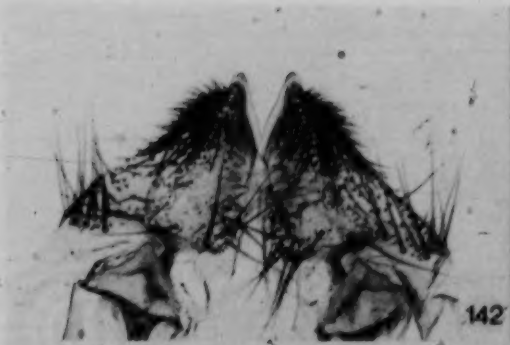
Figs. 142-149. Ovipositor valves of *Euxoa* spp., dorsal aspect. 142, *E. teleboa* (Sm.); 143, *E. moerens* (Grt.); 144, *E. latro* (B. & Benj.); 145, *E. murdocki* (Sm.); 146, *E. dodi* McD.; 147, *E. infracta* (Morr.); 148, *E. q. quadridentata* (Grt. & Rob.); 149, *E. quadridentata flutea* Sm. (Structures reproduced at about 32X).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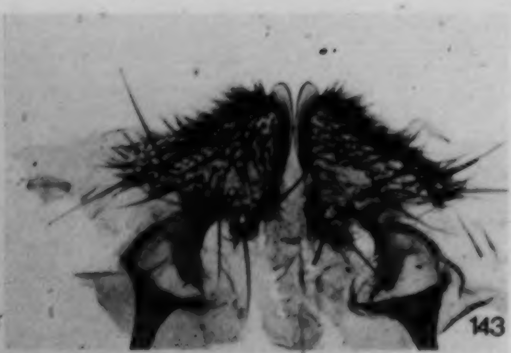
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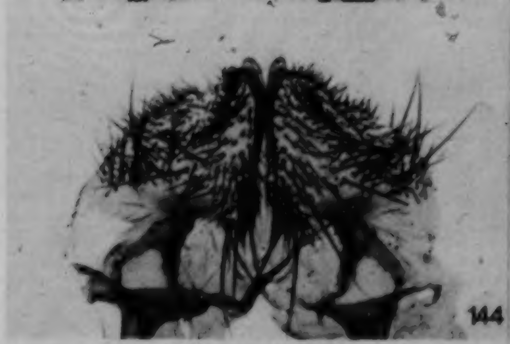
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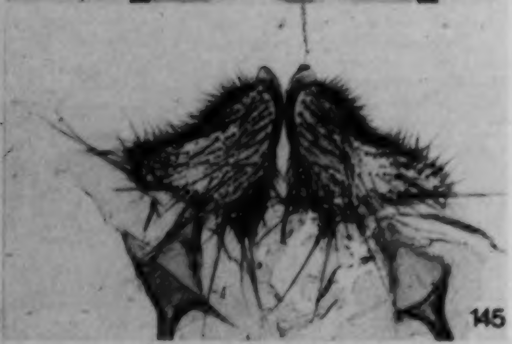
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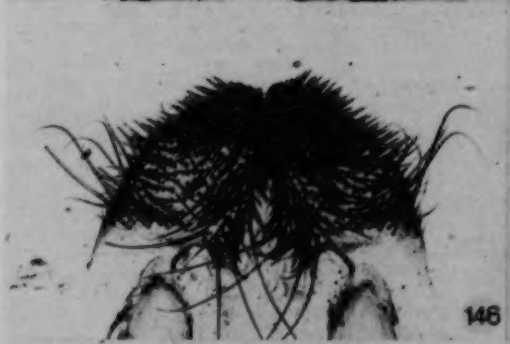
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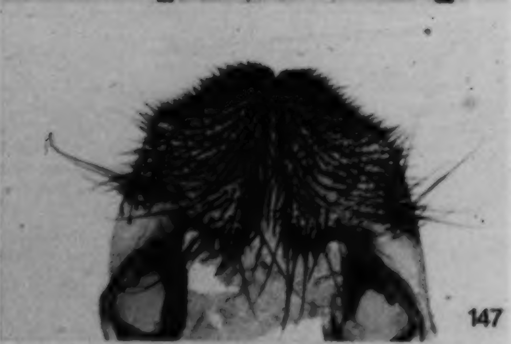
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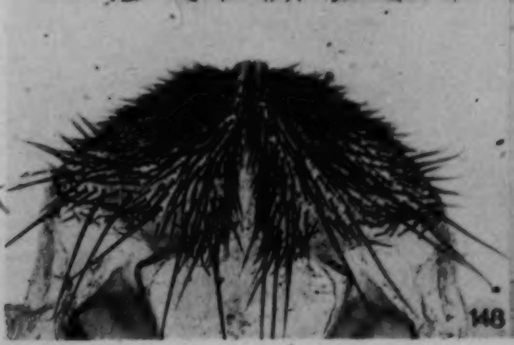
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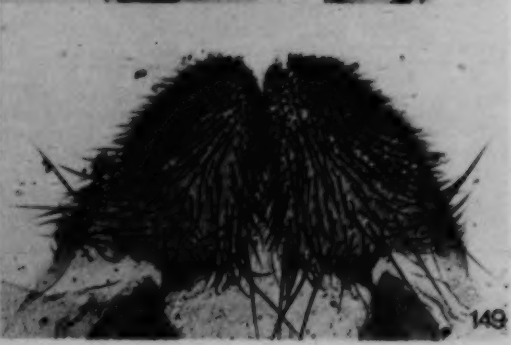
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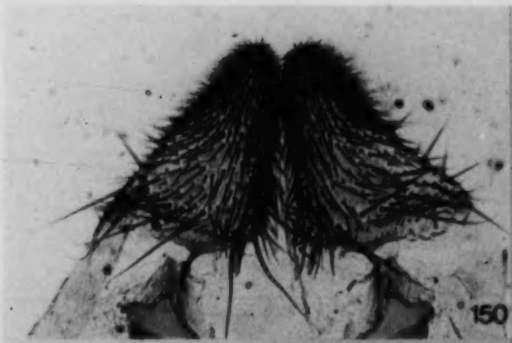
Figs. 150-157. Ovipositor valves of _Euxoa_ spp., dorsal aspect. 150, _E. laetificans_ (Sm.); 151, _E. inscripta_ Lafontaine, new species; 152, _E. niveilinea_ (Grt.); 153, _E. dargo_ (Stkr.); 154, _E. melura_ McD.; 155, _E. detersa_ (Wlk.); 156, _E. cicatricosa_ (Grt. & Rob.); 157, _E. recula_ (Harv.). (Structures reproduced at about 32X).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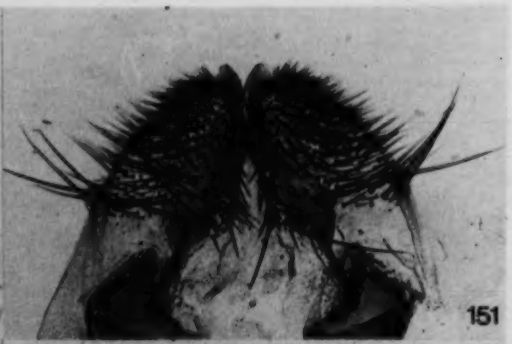
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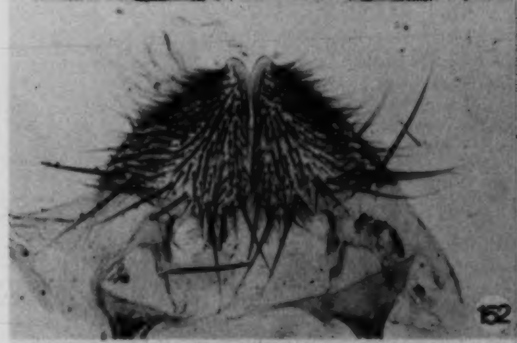
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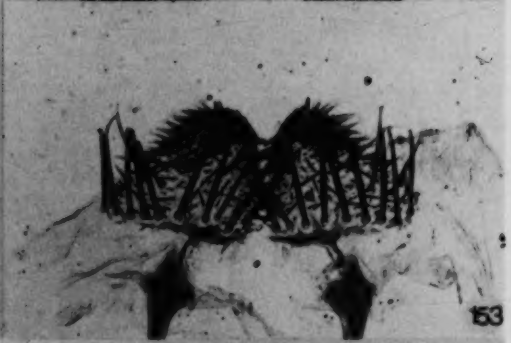
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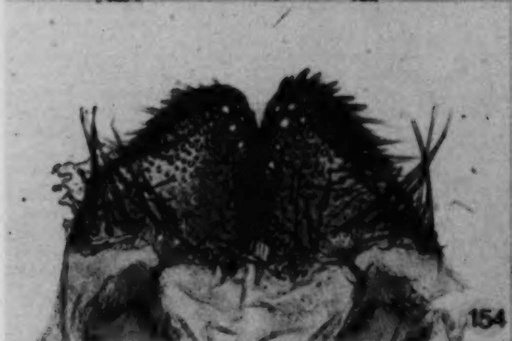
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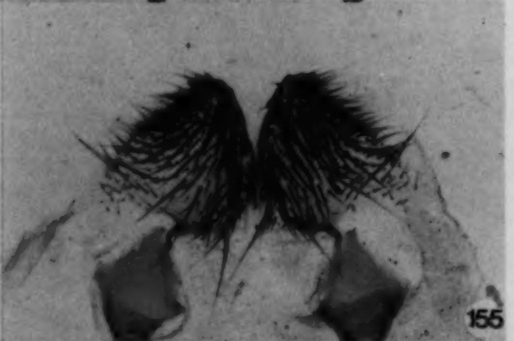
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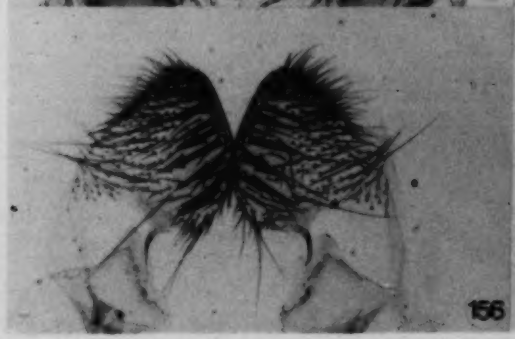
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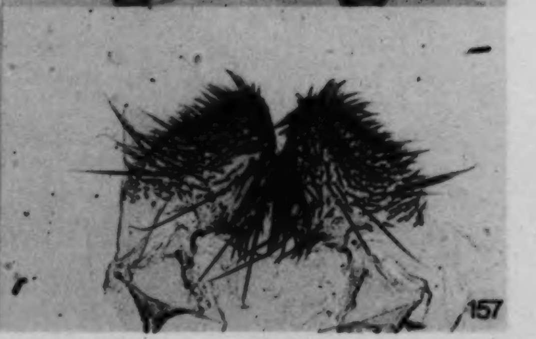
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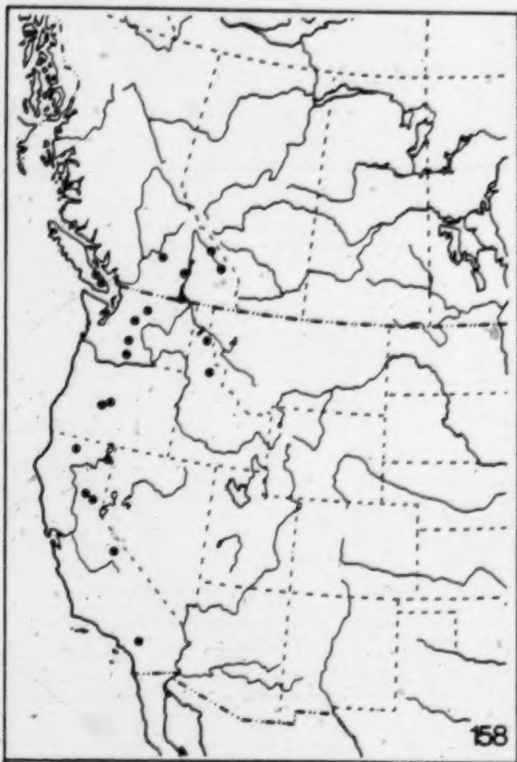
Figs. 158-161. Distribution of *Euxoa* spp. 158, *E. costata* (Grt.); 159, *E. castanea* Lafontaine, new species; 160, *E. idahoensis* (Grt.); 161, *E. foeminalis* (Sm.) (▲), *E. clausa* McD. (■).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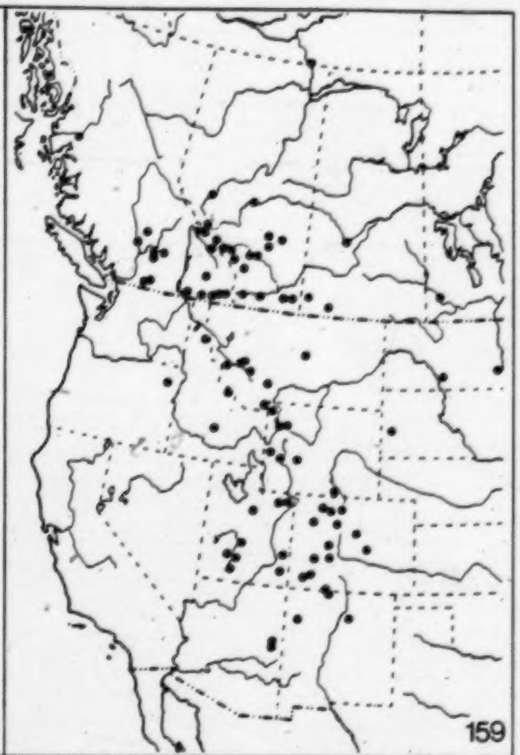
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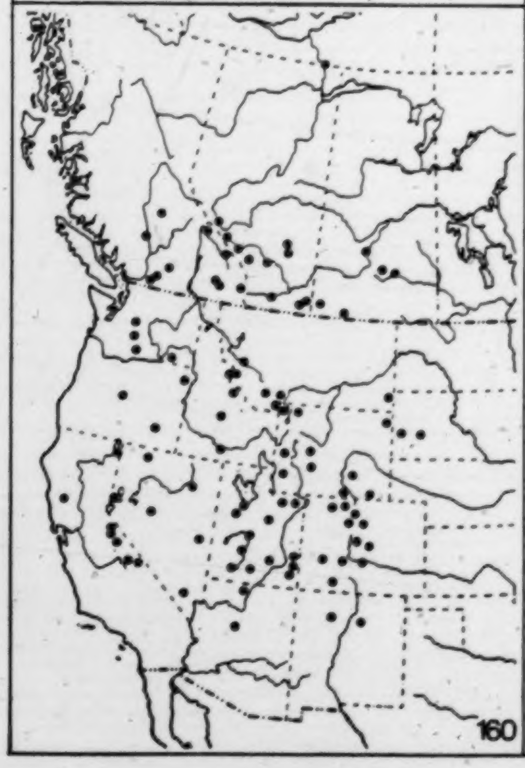
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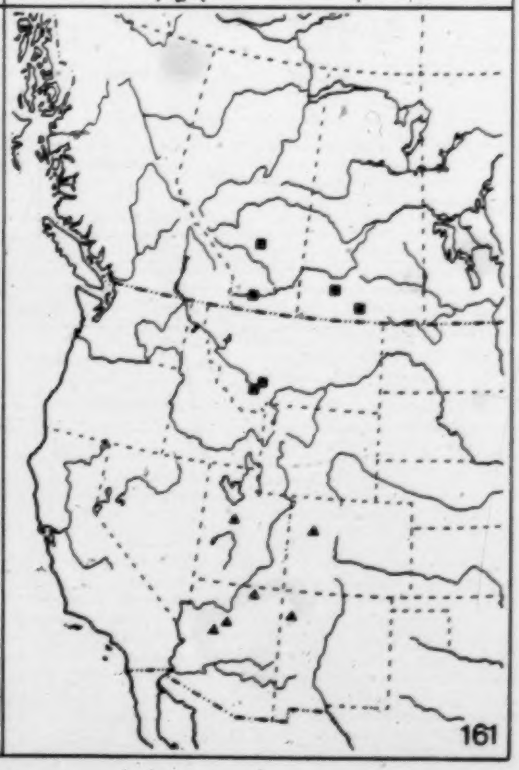
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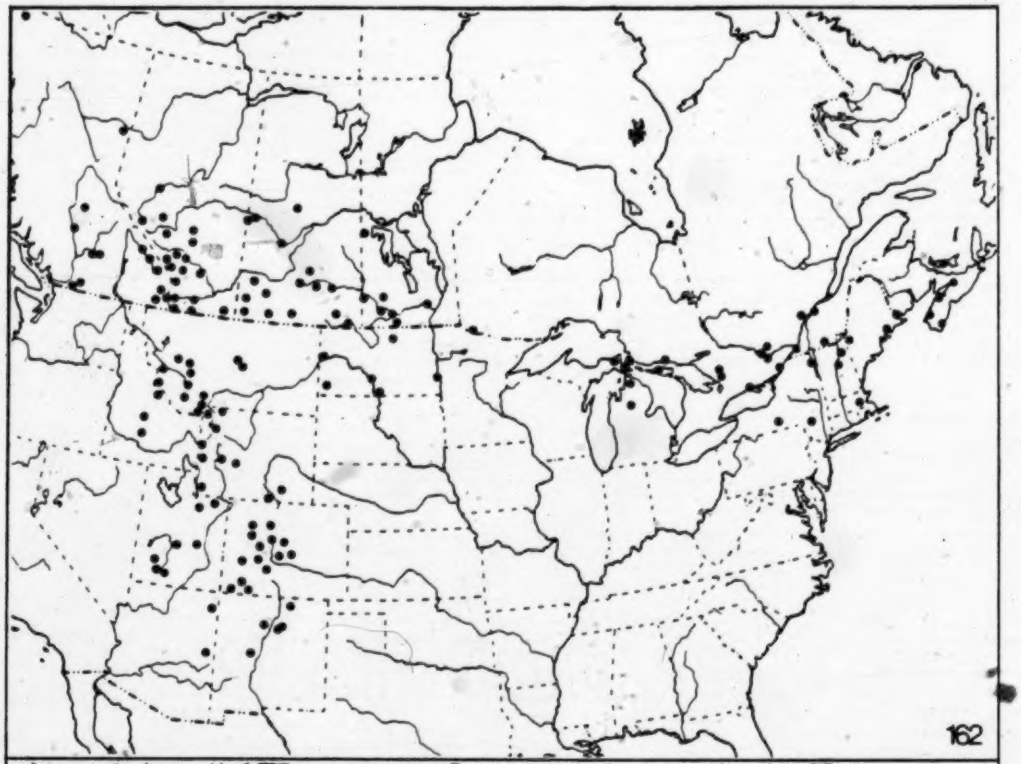
Figs. 162-163. Distribution of *Euxoa* spp. 162, *E. servita* (Sm.); 163, *E. redimicula* (Morr.).



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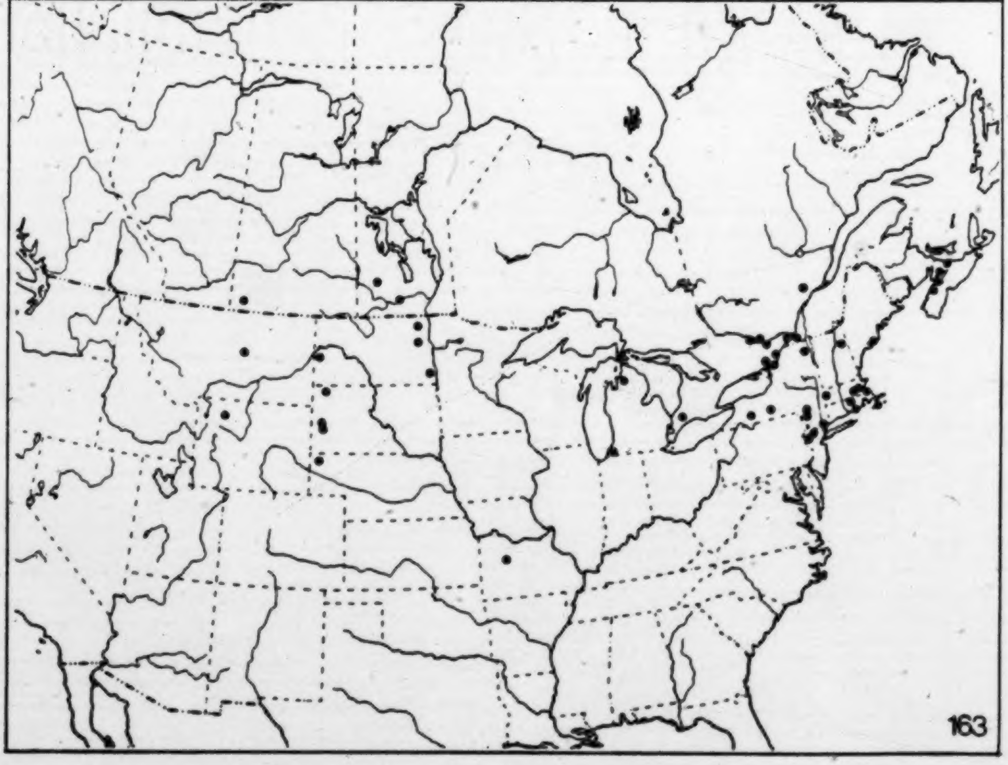

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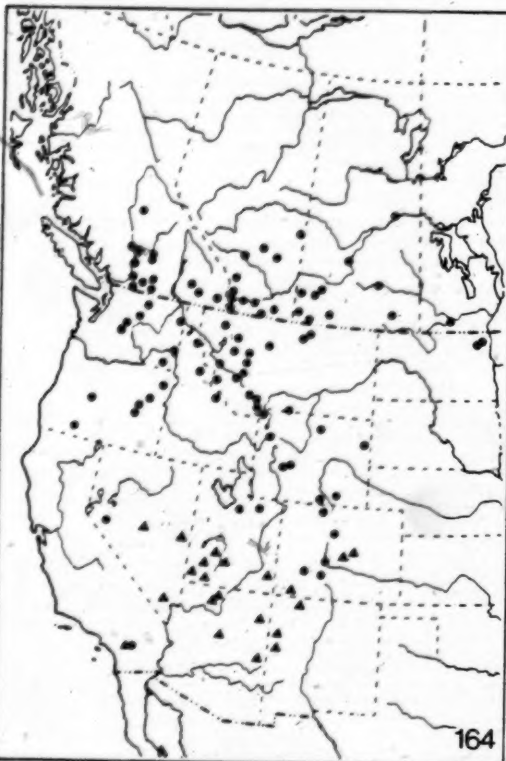
Figs. 164-167. Distribution of *Euxoa* spp. 164, *E. auripennis* Lafontaine (●), *E. arizonensis* Lafontaine (▲); 165, *E. olivalis* (Grt.); 166, *E. agema* (Stkr.); 167, *E. oblongistigma* (Sm.).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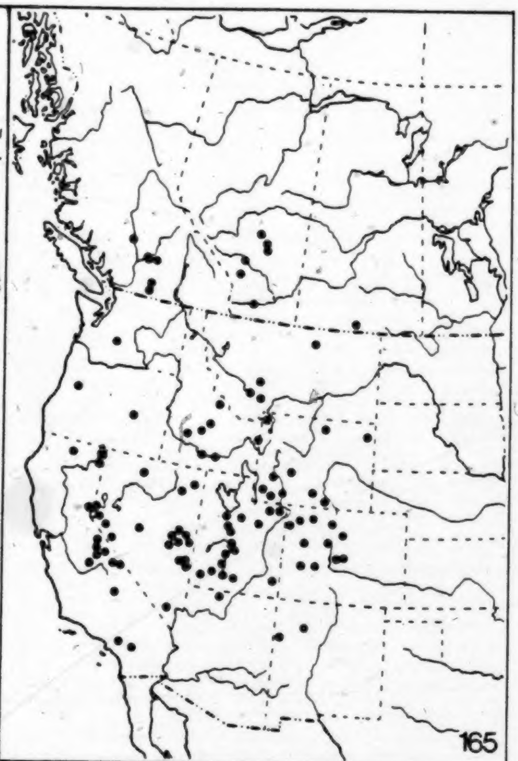
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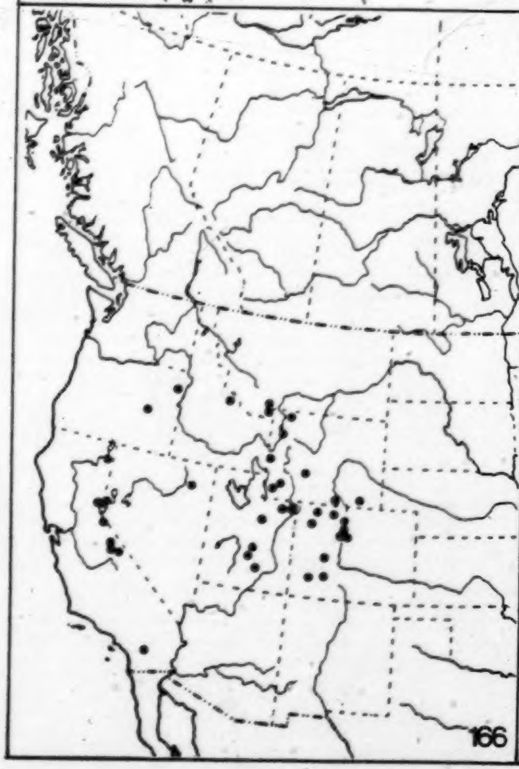
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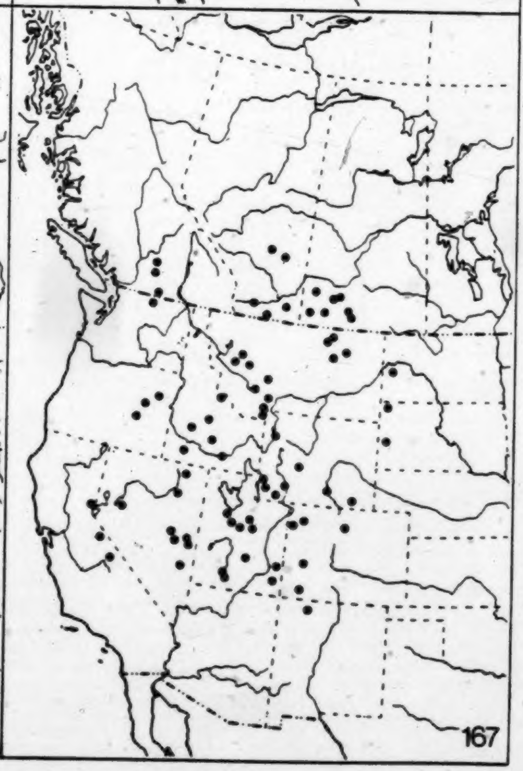
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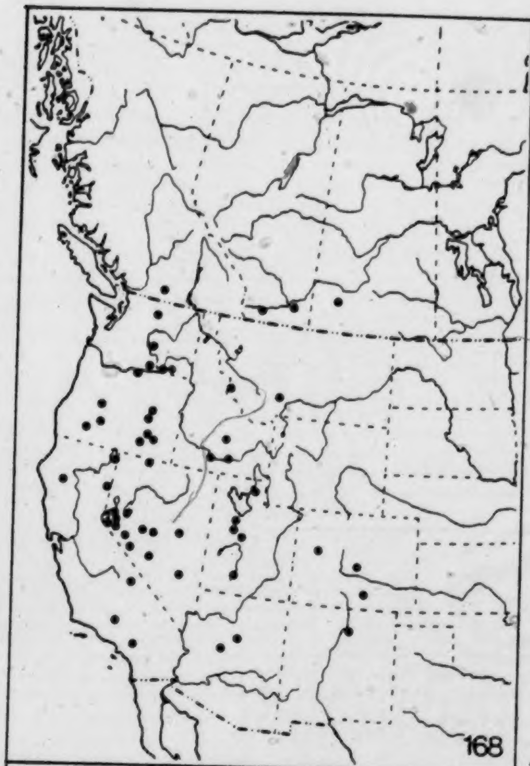
Figs. 168-171. Distribution of Euxoa spp. 168, E. brevipennis (Sm.); 169, E. citricolor (Grt.); 170, E. tronella (Sm.); 171, E. teleboa (Sm.).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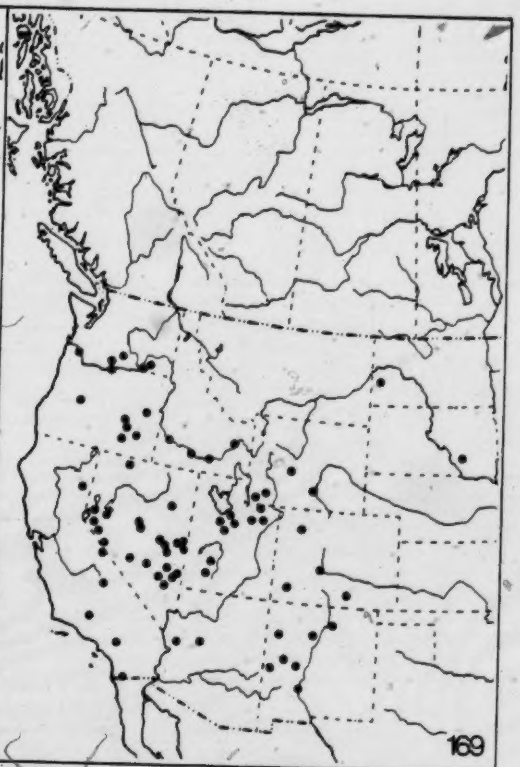
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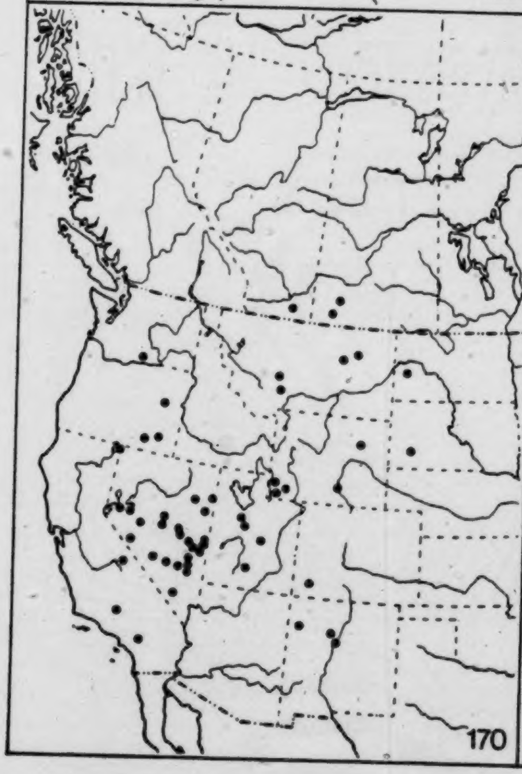
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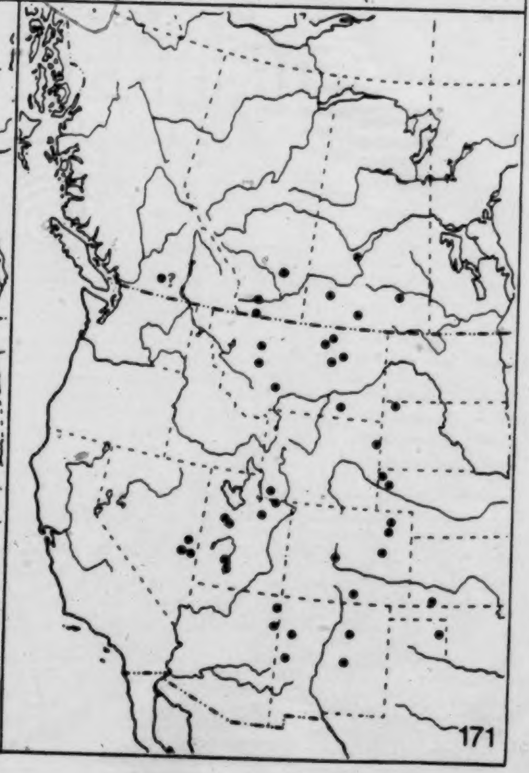
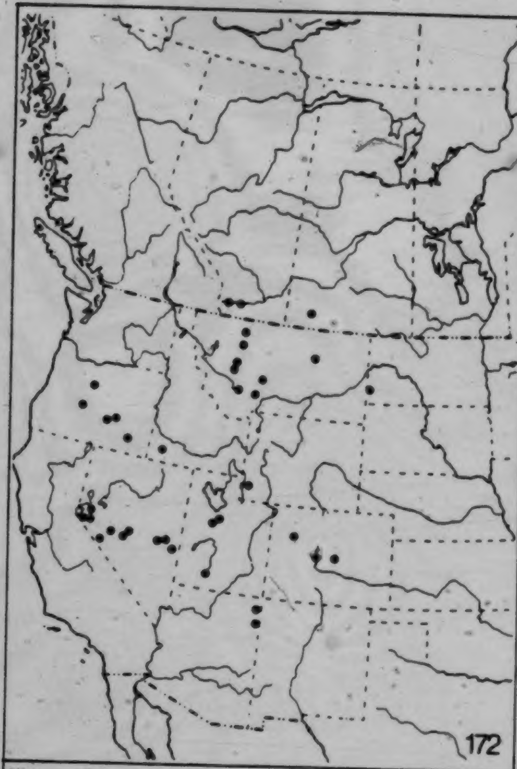
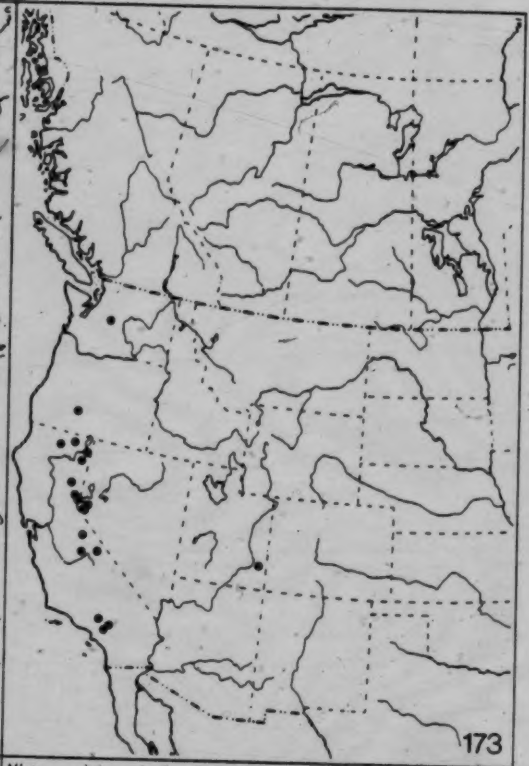


171

Figs. 172-175. Distribution of *Euxoa* spp. 172, *E. moerens* (Grt.); 173, *E. latro* (B. & Benj.); 174, *E. murdocki* (Sm.); 175, *E. dodi* McD.



172



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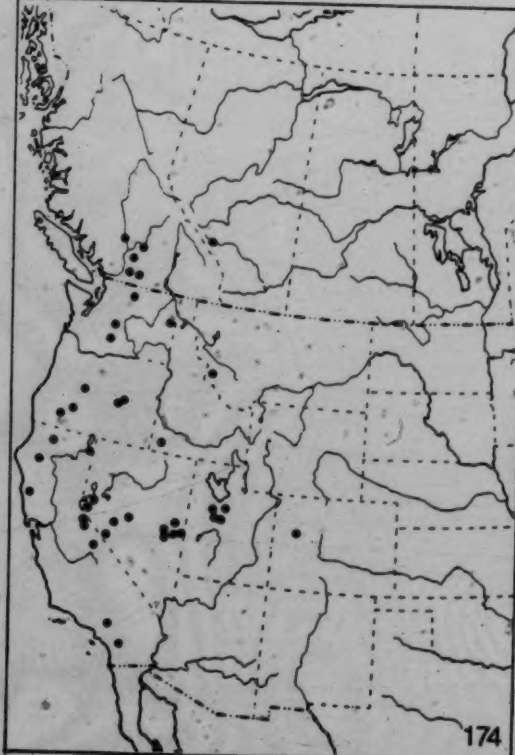
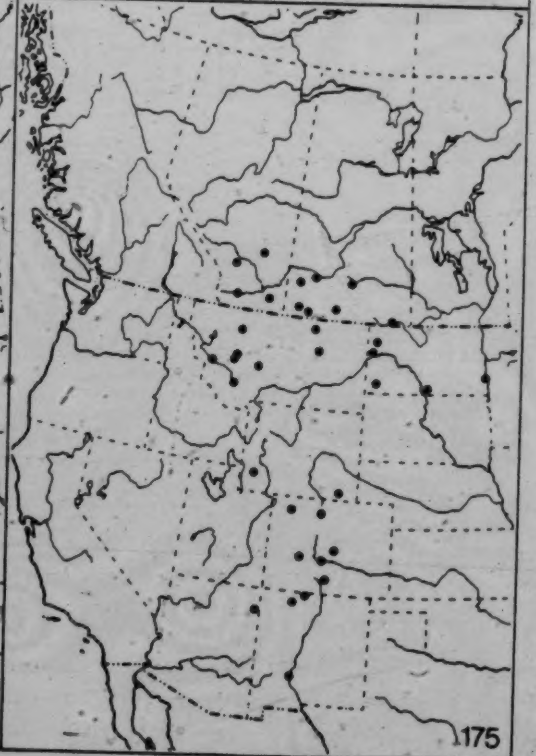
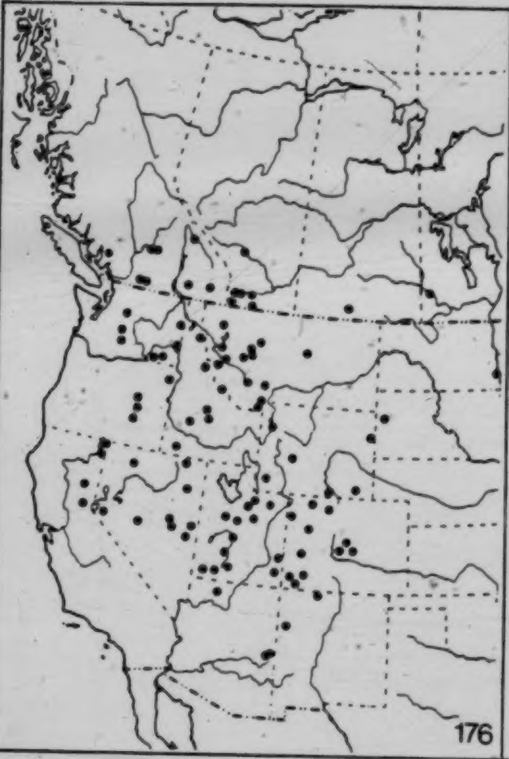


174

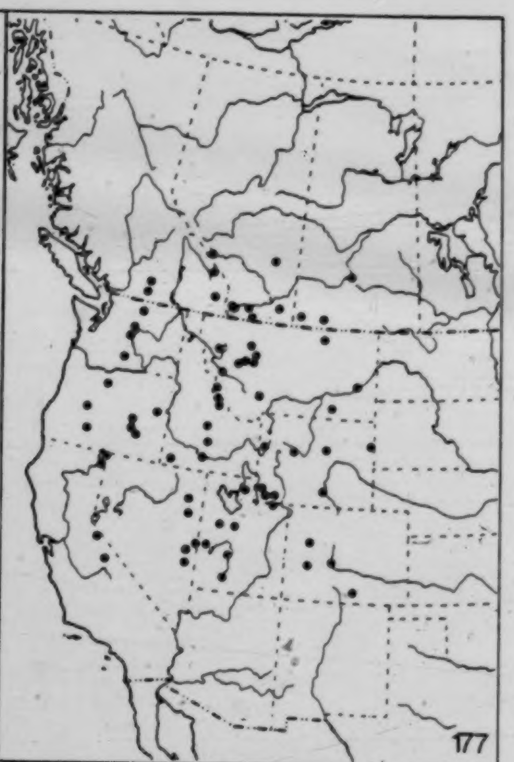


175

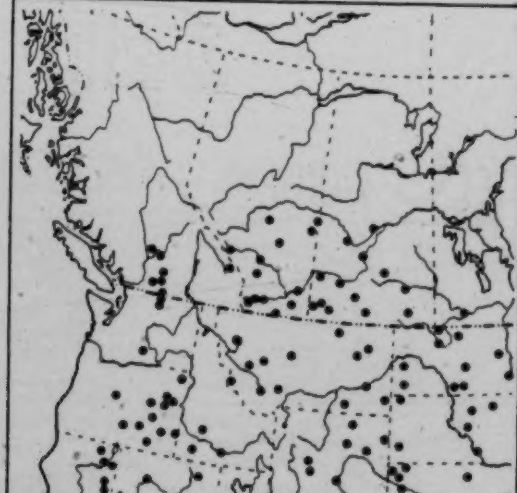
Figs. 176-179. Distribution of *Euxoa* spp. 176, *E. infracta* (Morr.); 177, *E. laetificans* (Sm.); 178, *E. quadridentata* (Grt. & Rob.); 179, *E. inscripta* Lafontaine, new species (●), *E. unica* McD. (■).



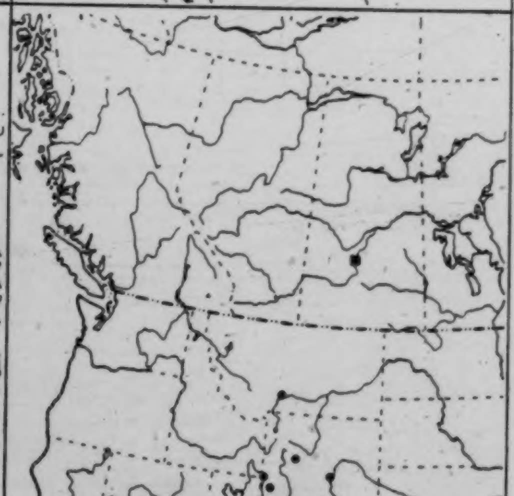
176



177

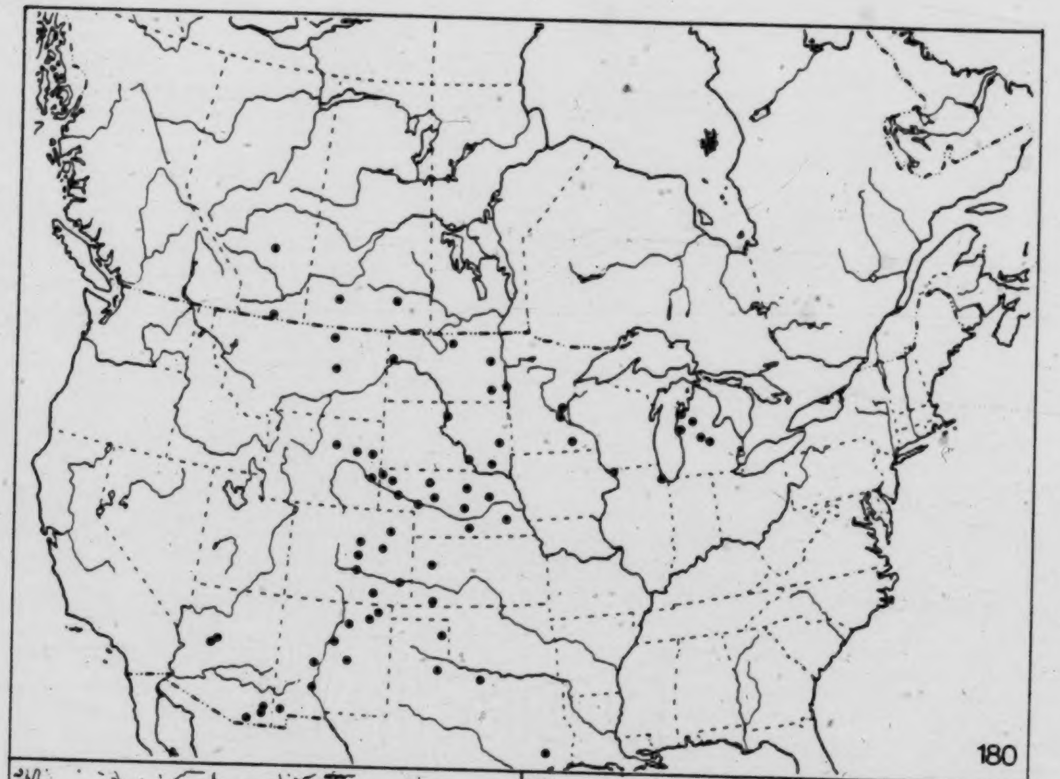


178



179

Figs. 180-182. Distribution of _Euxoa_ spp. 180, _E. niveilinea_ (Grt.); 181, _E. dargo_ (Stkr.); 182, _E. melura_ McD.



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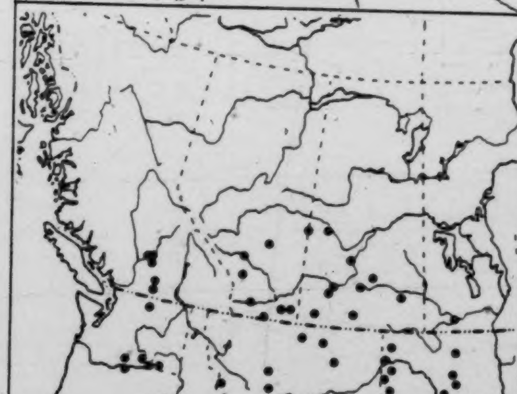
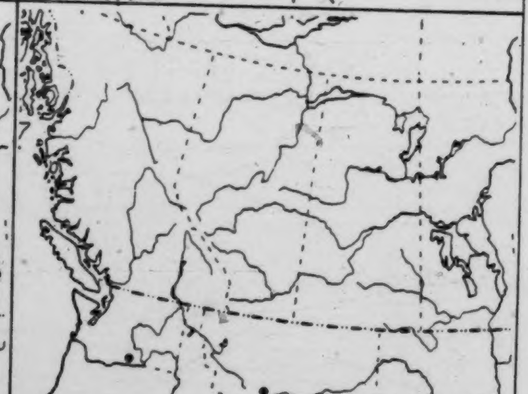
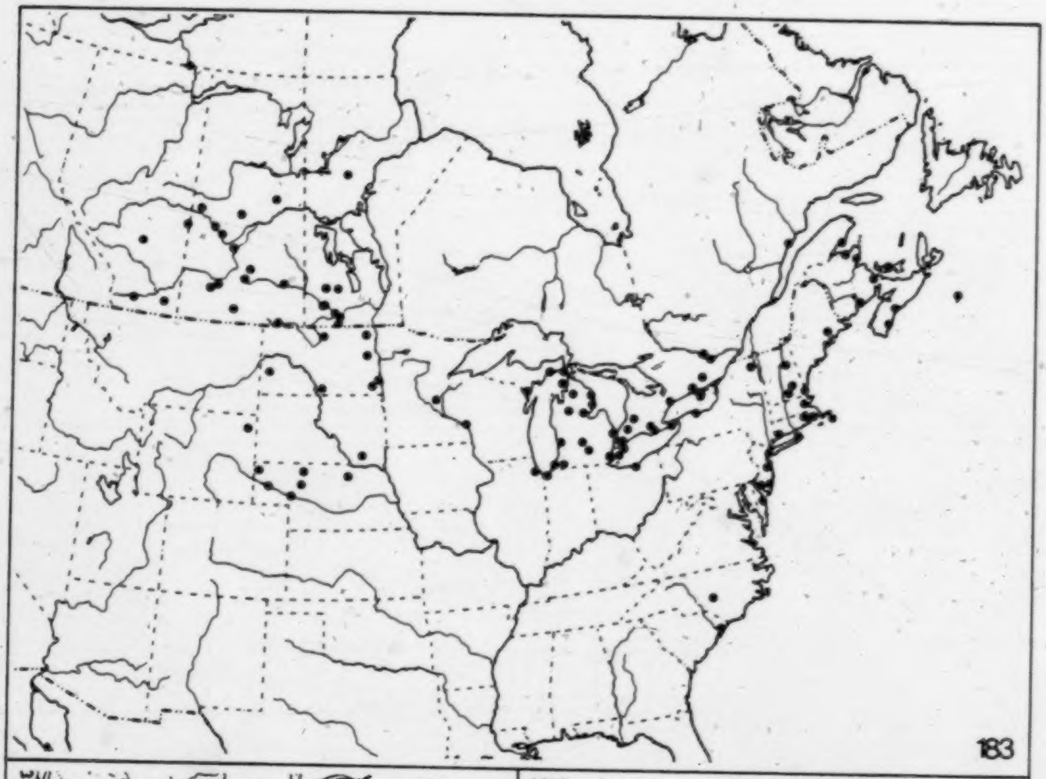


181

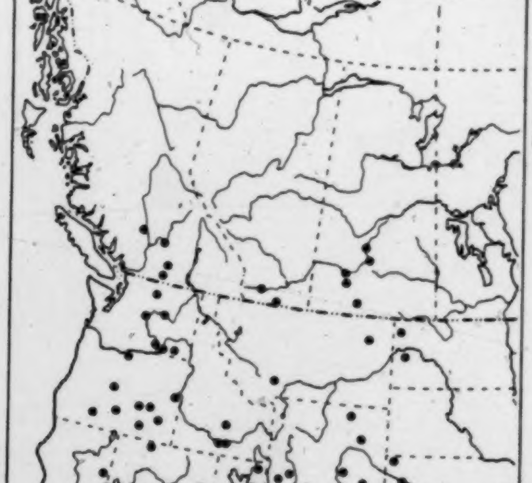


182

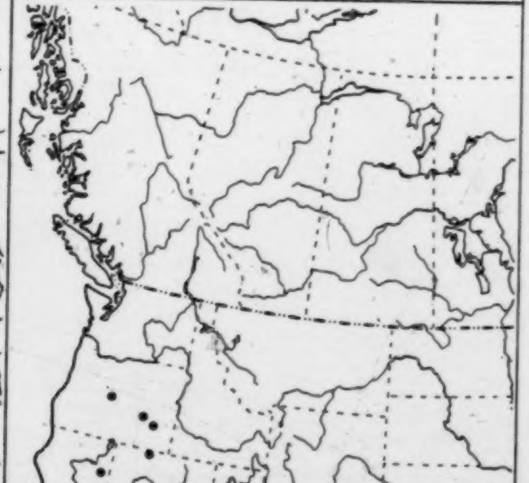
Figs. 183-185. Distribution of *Euxoa* spp. 183, *E. detersa* (Wlk.); 184, *E. cicatricosa* (Grt. & Rob.); 185, *E. recula* (Harv.).



183



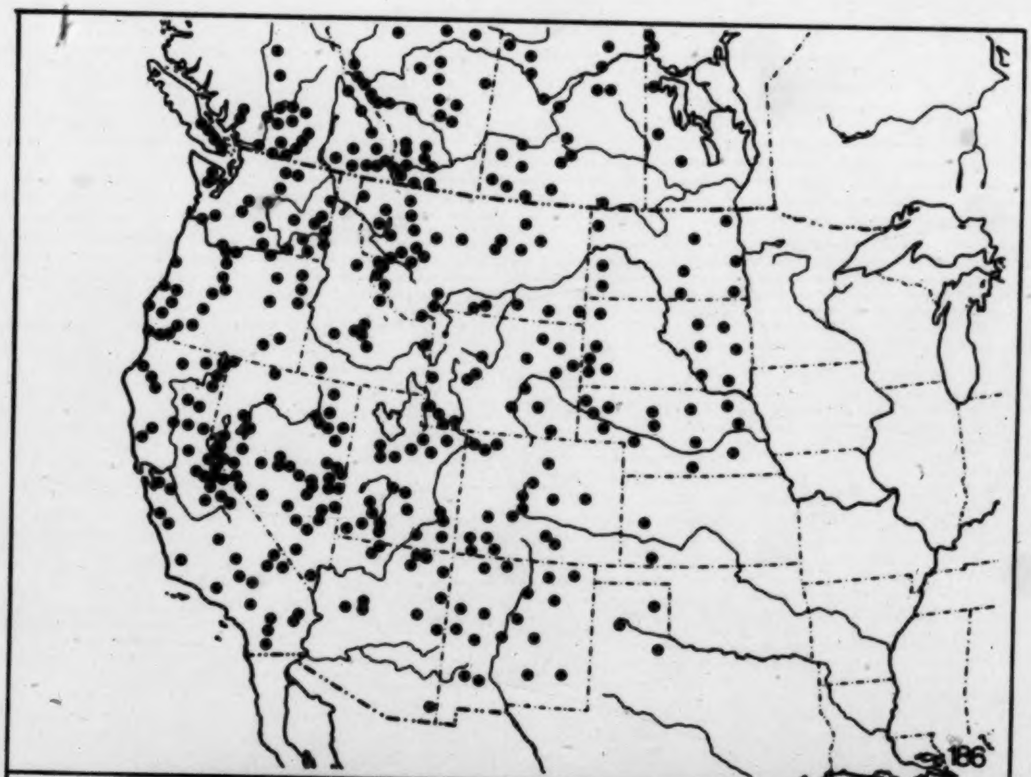
184



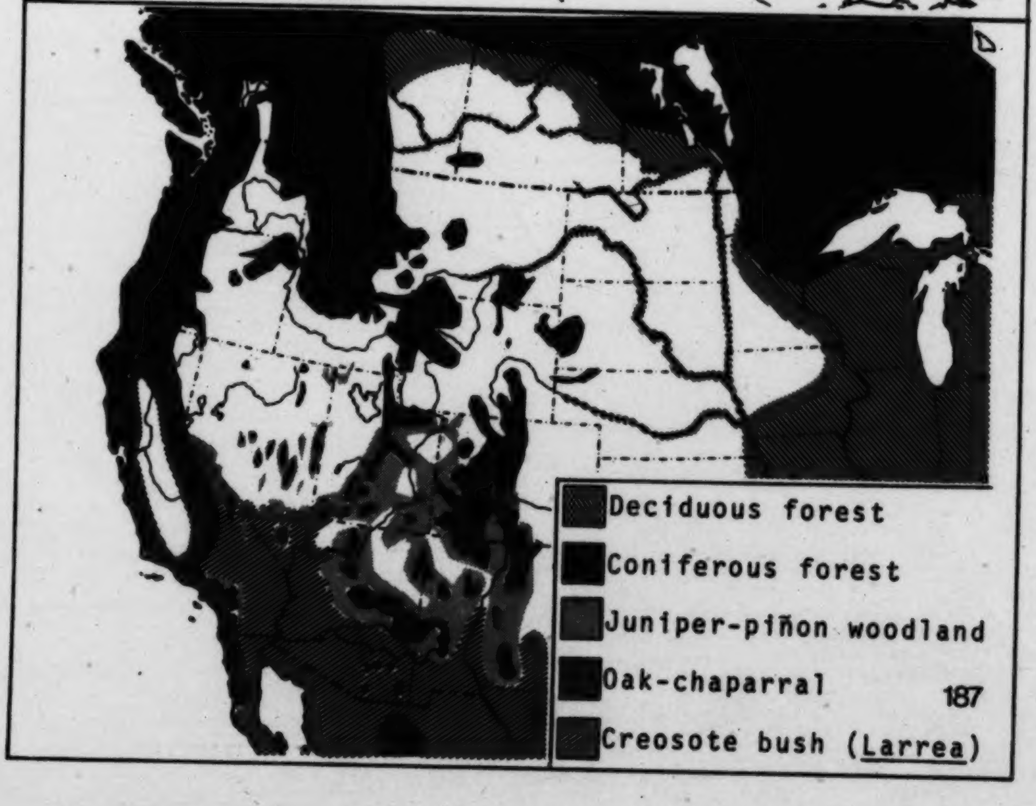
185

Fig. 186. Distribution of localities at which collections were made during survey of Euxoa in western North America.

Fig. 187. Distribution of major vegetation zones of western North America. (Grassland and sagebrush areas and bodies of water are unshaded).



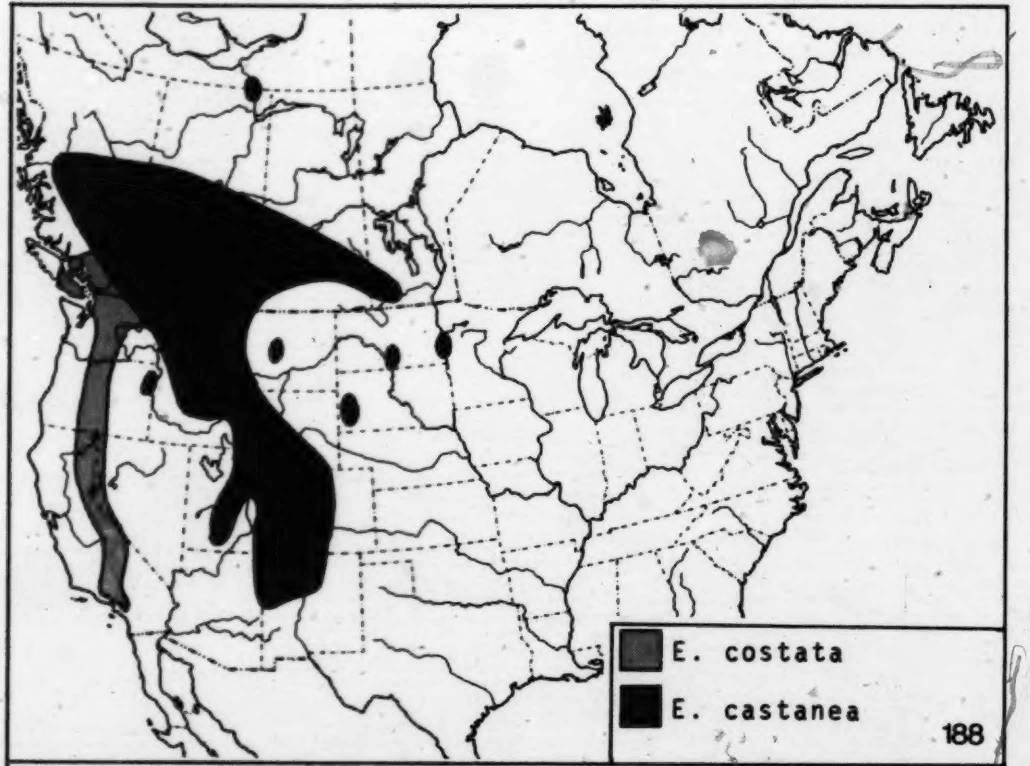
186



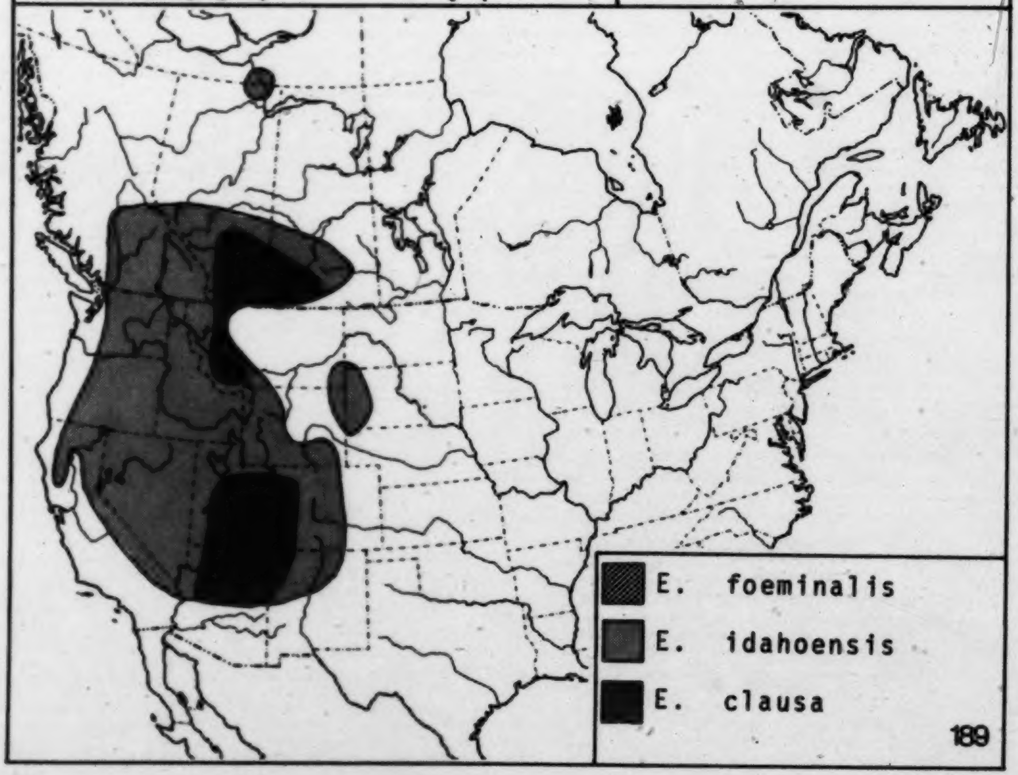
Deciduous forest
Coniferous forest
Juniper-piñon woodland
Oak-chaparral
Creosote bush (Larrea)

187

Figs. 188-189. Ranges of sister species of Euxoa detersa group. 188, E. costata (Grt.), E. castanea Lafontaine, new species; 189, E. foeminalis (Sm.), E. idahoensis (Grt.), E. clausa McD.

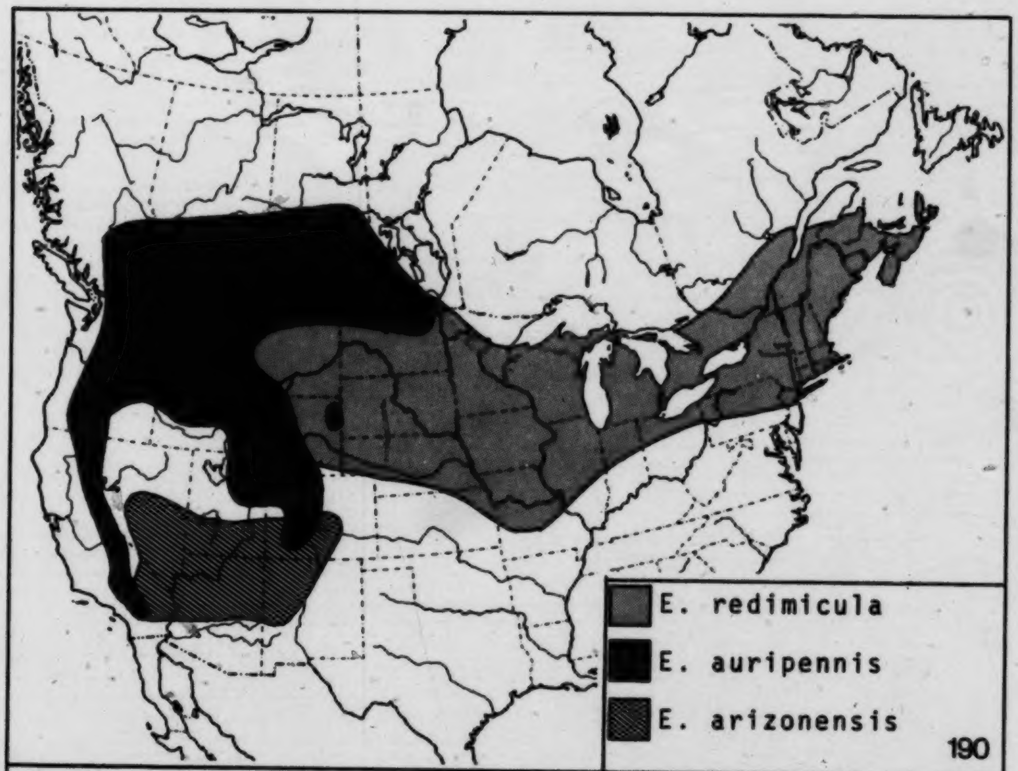

▨ E. costata
■ E. castanea

188

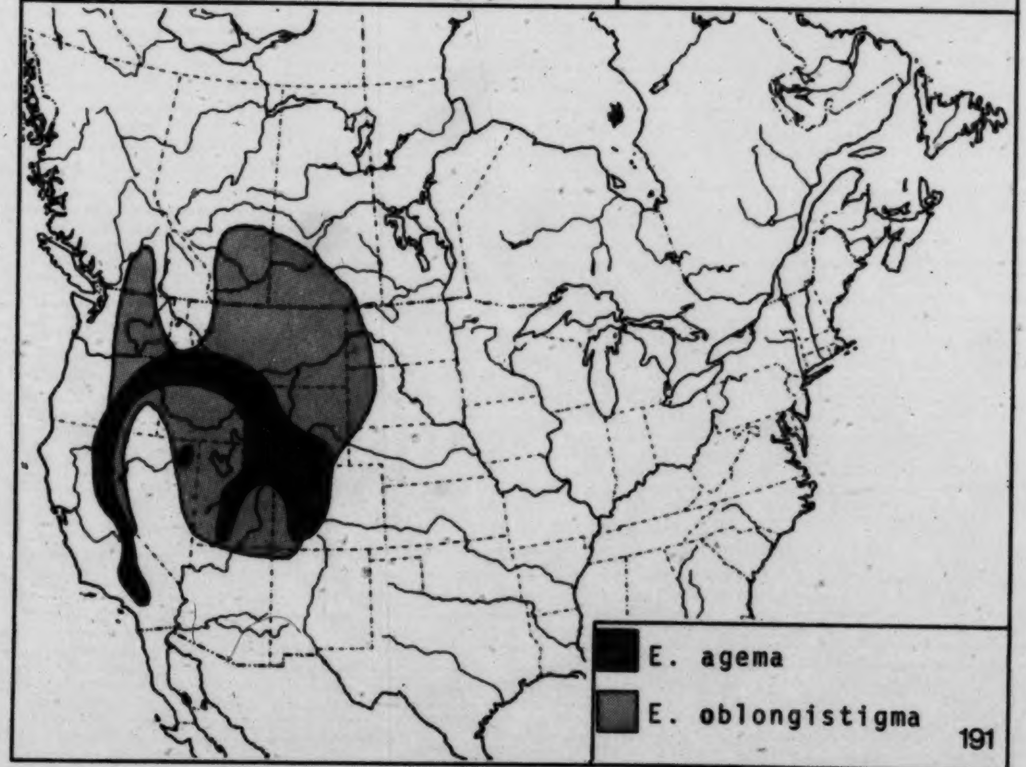

▨ E. foeminalis
▨ E. idahoensis
■ E. clausa

189

Figs. 190-191. Ranges of sister species of *Euxoa detersa* group. 190, *E. redimicula* (Morr.), *E. auripennis* Lafontaine, *E. arizonensis* Lafontaine; 191, *E. agema* (Stkr.), *E. oblongistigma* (Sm.).

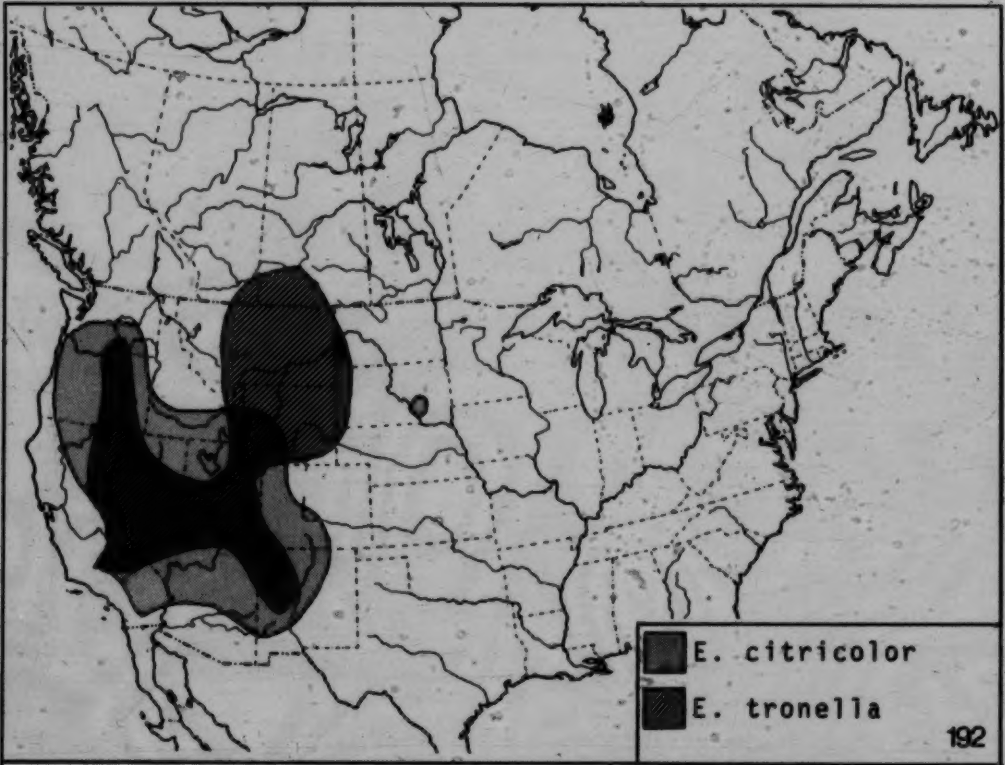

E. redimicula
E. auripennis
E. arizonensis

190

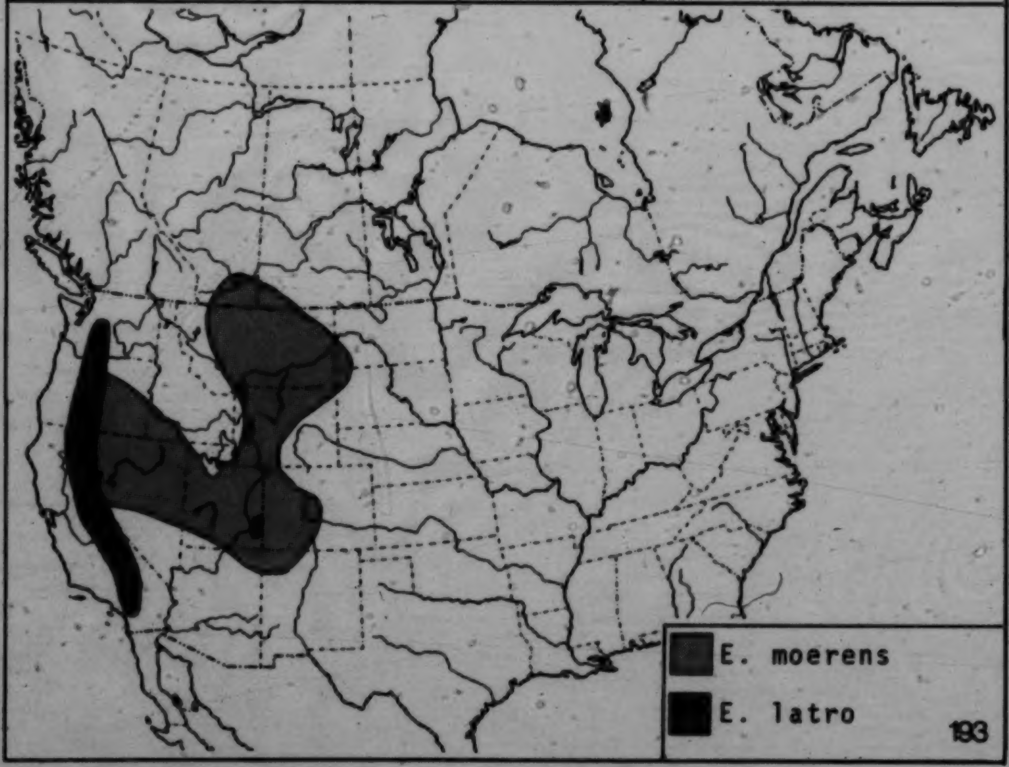

E. agema
E. oblongistigma

191

Figs. 192-193. Ranges of sister species of Euxoa detersa group. 192, E. citricolor (Grt.), E. tronella (Sm.); 193, E. moerens (Grt.), E. latro (B. & Benj.).

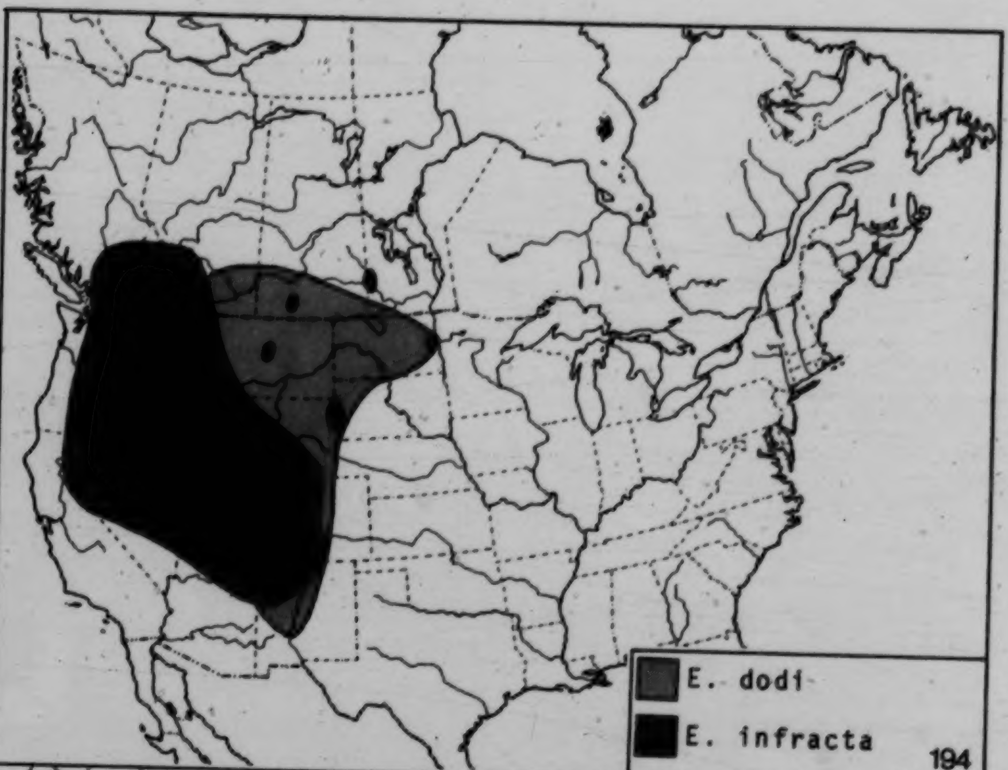

E. citricolor
E. tronella

192

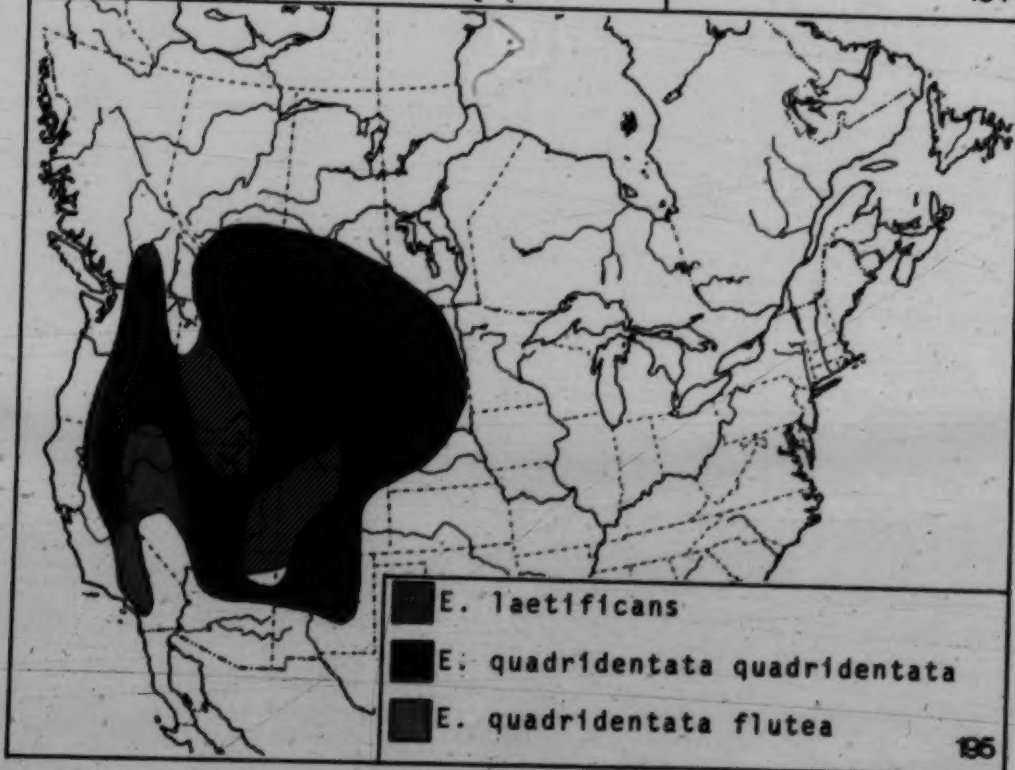

E. moerens
E. latro

193

Figs. 194-195. Ranges of sister species of Euxoa detersa group. 194, E. dodi McD., E. infracta (Morr.); 195, E. laetificans (Sm.), E. q. quadridentata (Grt. & Rob.), E. quadridentata flutea Sm.

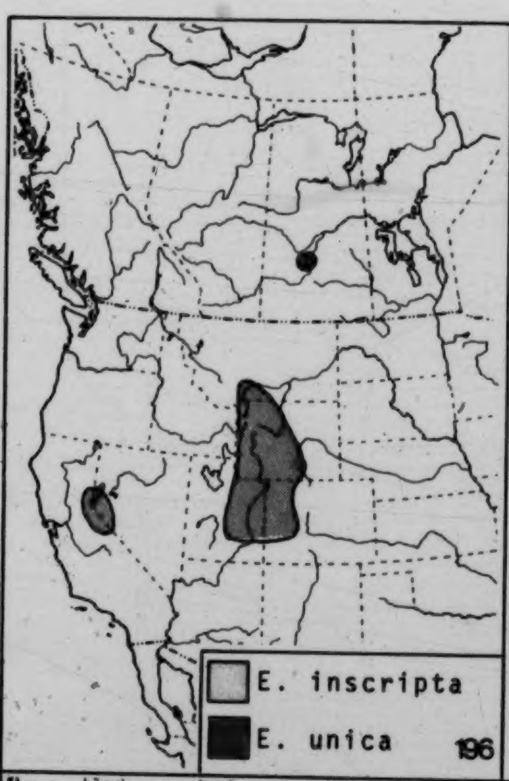

E. dodi
E. infracta

194

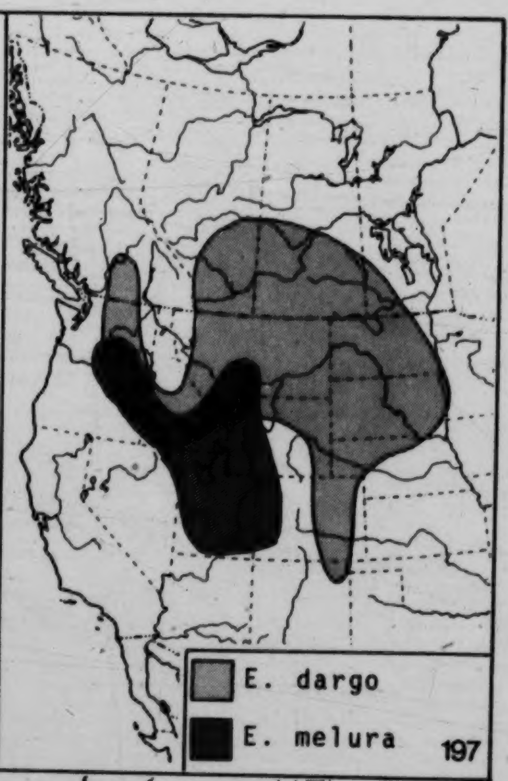

E. laetificans
E. quadridentata quadridentata
E. quadridentata flutea

195

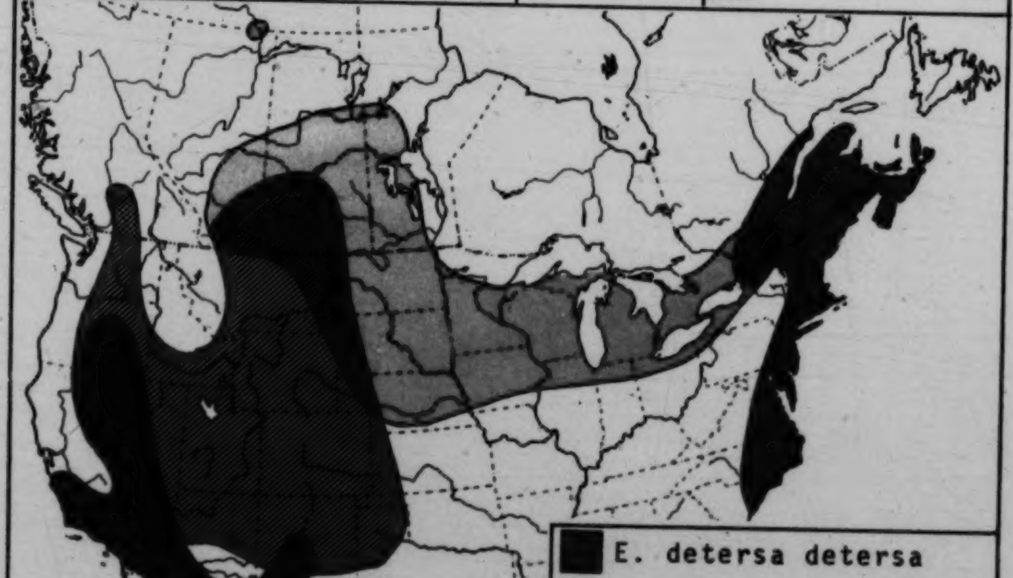
Figs. 196-198. Ranges of sister species of *Euxoa detersa* group. 196, *E. inscripta* Lafontaine, new species, *E. unica* McD.; 197, *E. dargo* (Stkr.), *E. melura* McD.; 198, *E. d. detersa* (Wlk.), *E. detersa personata* (Morr.), *E. cicatricosa* (Grt. & Rob.), *E. recula* (Harv.).


E. inscripta
E. unica

196

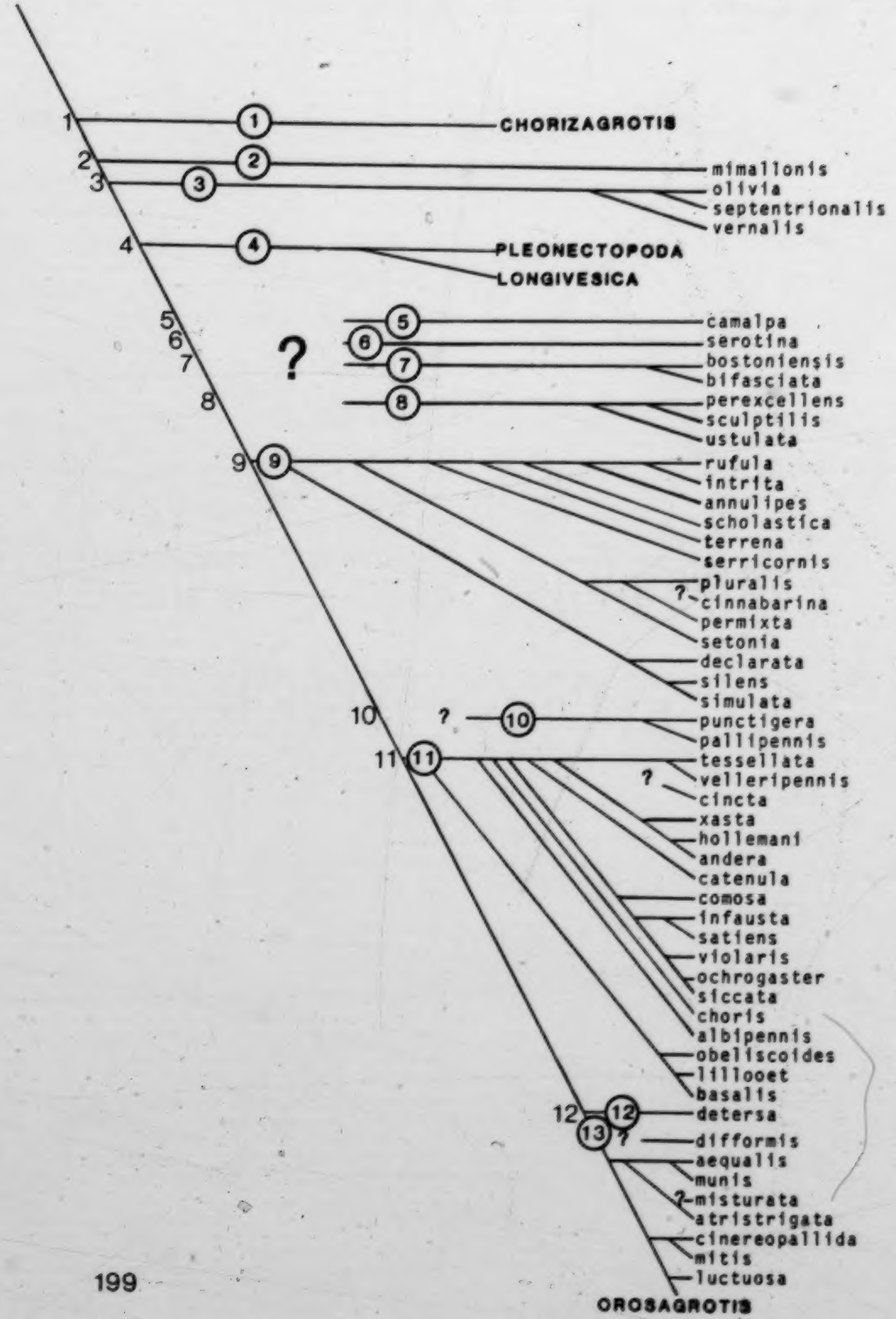

E. dargo
E. melura

197


E. detersa detersa
E. detersa personata
E. cicatricosa
E. recula

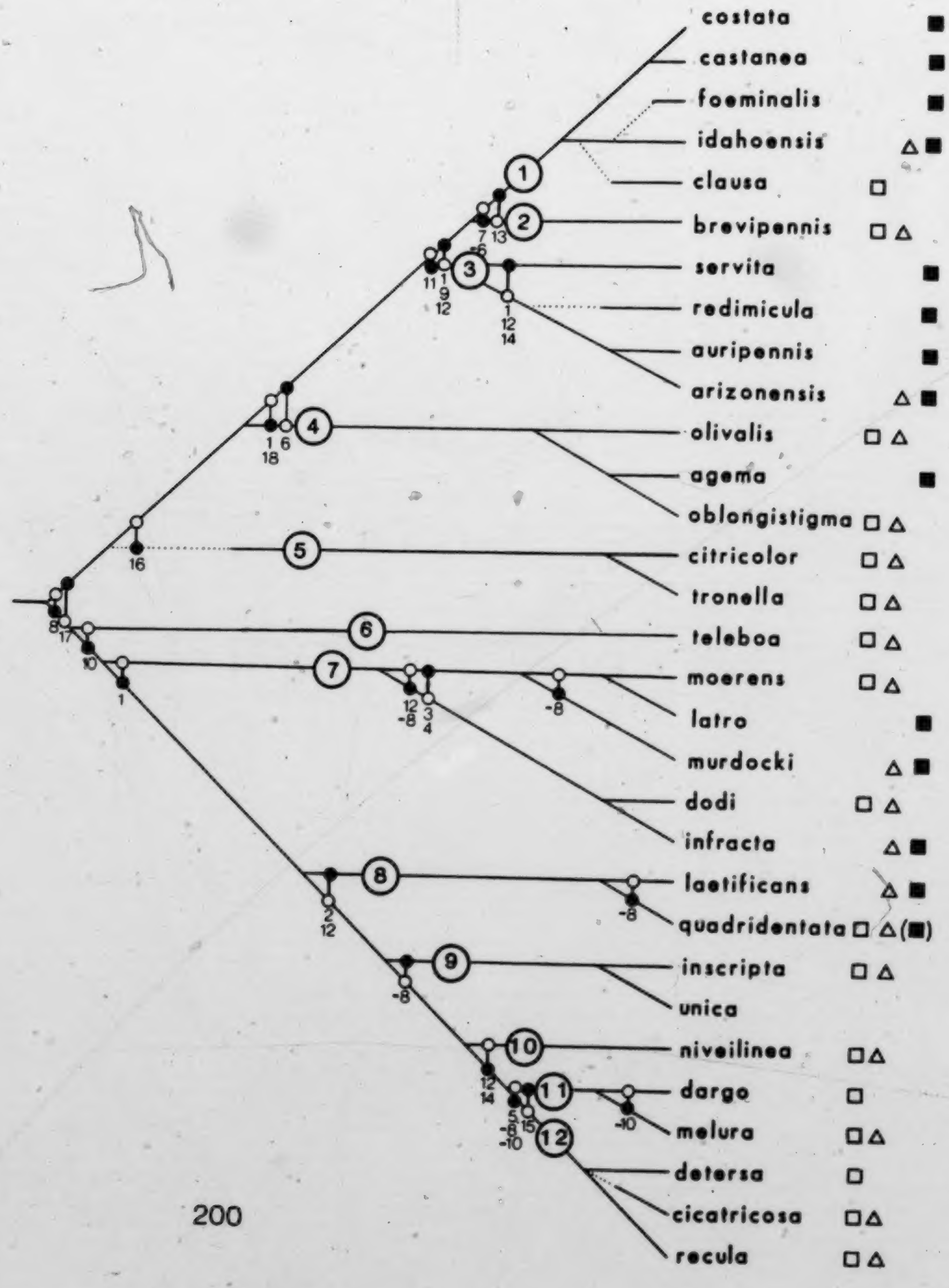
198

Fig. 199. Reconstructed phylogeny of subgenera and species groups of Euxoa.


1
①
CHORIZAGROTIS
2
②
mimallonis
3
③
olivia
septentrionalis
vernalis
4
④
PLEONECTOPODA
LONGIVESICA
5
⑤
camalpa
6
⑥
serotina
?
7
⑦
bostoniensis
bifasciata
8
⑧
perexcellens
sculptilis
ustulata
9
⑨
rufula
intrita
annulipes
scholastica
terrena
serricornis
pluralis
?
cinnabarina
permixta
setonia
declarata
silens
simulata
10
?
⑩
punctigera
pallipennis
11
⑪
tessellata
velleripennis
?
cincta
xasta
hollemani
andera
catenula
comosa
infausta
satiens
violaris
ochrogaster
siccata
choris
albipennis
obeliscoides
lillooet
basalis
12
⑫
detersa
⑬
?
difformis
aequalis
munis
?
misturata
atristrigata
cinereopallida
mitis
luctuosa
OROSAGROTIS

199

Fig. 200. Reconstructed phylogeny and habitat of species of *Euxoa detersa* group. Circled numbers are lineages described in text. Small numbers represent characters listed in tables 2 and 3 (negative numbers represent the secondary loss of derived character states). Habitat symbols: □, open aridlands; △, piñon-juniper woodland; ■, conifer forest.


costata ■
castanea ■
foeminalis ■
idahoensis △■
clausa □
brevipennis □△
servita ■
redimicula ■
auripennis ■
arizonensis △■
olivalis □△
agema ■
oblongistigma □△
citricolor □△
tronella □△
teleboa □△
moerens □△
latro ■
murdocki △■
dodi □△
infracta △■
laetificans △■
quadridentata □△(■)
inscripta □△
unica
niveilinea □△
dargo □
melura □△
detersa □
cicatricosa □△
recula □△
1
2
3
4
5
6
7
8
9
10
11
12

200

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